Reefs that defy the heat: identifying naturally resilient and hypersensitive coral communities from four decades of global bleaching and satellite temperature records

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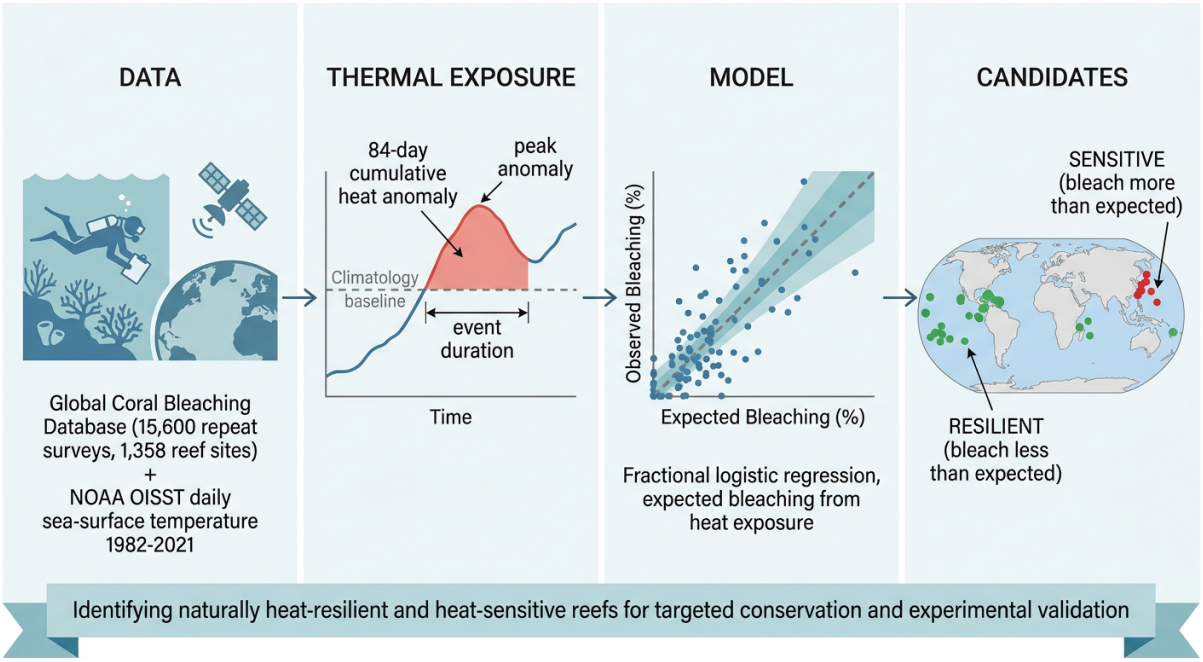

Graphical abstract. A residual-based framework couples the Global Coral Bleaching Database with daily NOAA OISST v2.1 temperature to predict expected bleaching from antecedent heat exposure. Reefs that bleach far less than expected (resilient "winners") cluster in the central-equatorial Pacific; reefs that bleach far more than expected (sensitive "losers") cluster in the Ryukyu Islands of southern Japan. Candidates feed a targeted validation programme of in-situ loggers, symbiont profiling, and standardized heat-tolerance assays.

Abstract

Marine heatwaves now drive recurrent mass coral bleaching, yet reefs vary enormously in how severely they bleach for a given thermal dose. Locating the reefs that consistently over- or under-perform relative to their heat exposure is a prerequisite for both climate-refugia conservation and for the mechanistic study of thermal tolerance. We integrated the Global Coral Bleaching Database (33 244 surveys, 1963–2021) with daily 0.25° NOAA Optimum Interpolation Sea Surface Temperature (OISST v2.1, 1982–2021) to quantify, for every survey, the antecedent thermal stress experienced over the preceding 84 days relative to a site-specific 1982–2011 daily climatology. Restricting the analysis to 15 600 surveys at 1358 repeatedly monitored reef clusters, we fitted a

fractional logistic regression that predicts the *expected* proportion of a colony assemblage bleached from three thermal-exposure metrics (cumulative positive anomaly, peak anomaly, event duration) together with region and year effects. Cumulative heat accumulation was the dominant predictor (odds ratio 2.23 per standard deviation, $p < 10^{-38}$), and the model generalized to spatially held-out reefs (leave-site-out mean absolute error 15.0%). The residual (observed minus expected bleaching) isolates the response not explained by measured heat or biogeography. Aggregating residuals across repeat visits and ranking 1223 sites, we identify 30 resilient and 30 sensitive candidate reefs, 28 of which are significant after false-discovery-rate correction. Resilient reefs cluster in the central-equatorial Pacific (Phoenix and Line Islands, Kiribati), consistent with equatorial upwelling and advective cooling, whereas the most extreme sensitive reefs cluster in the semi-enclosed lagoons of the Ryukyu/Yaeyama Islands, where several sites bleached ∼100% while satellite temperature predicted only ∼4% — a textbook signature of sub-grid heat that a coarse satellite product cannot resolve. We provide the ranked candidate lists and a validation programme using high-frequency temperature loggers, ITS2 symbiont metabarcoding, and Coral Bleaching Automated Stress System (CBASS) assays designed to discriminate genuine holobiont tolerance from thermal-exposure measurement error.

Keywords: coral bleaching; thermal refugia; marine heatwaves; resilience; Symbiodiniaceae; sea surface temperature; fractional logistic regression

1 Introduction

Reef-building corals persist within a narrow thermal envelope, and their obligate symbiosis with dinoflagellate algae of the family Symbiodiniaceae collapses when temperatures exceed the local summer maximum by only 1–2 °C for a sustained period (Hoegh-Guldberg, 1999; LaJeunesse et al., 2018). The visible endpoint of this collapse — coral bleaching — reflects the breakdown of nutrient exchange and the expulsion or degradation of the algal symbionts under heat and light stress (Rädecker et al., 2021; van Woesik et al., 2022). Since the first documented pan-tropical event in 1982–1983, mass bleaching has become progressively more frequent and severe, and it is now recognised as the foremost climate-driven threat to the persistence of coral reef ecosystems worldwide (Hughes et al., 2017, 2018a; Eakin et al., 2019). During the 2015–2016 global event, more than three times as many reefs were exposed to bleaching-level heat stress as during the 1998 event, and heat exposure exceeding critical thresholds drove immediate mortality and lasting shifts in community composition across entire regions (Eakin et al., 2019; Hughes et al., 2018b). Global syntheses confirm that bleaching probability rises steeply with the intensity and frequency of thermal-stress anomalies, although the response is far from uniform in space (Sully et al., 2019; McClanahan et al., 2020).

That spatial non-uniformity is the crux of the present study. Even within a single heatwave, neighbouring reefs experiencing similar satellite-derived temperatures can diverge dramatically in bleaching severity, producing a mosaic of ecological "winners and losers" (McClanahan et al., 2020; Sully et al., 2019). Some of this heterogeneity reflects genuine differences in the biological tolerance of the coral holobiont: populations with a history of exposure to variable temperature regimes can be physiologically pre-conditioned, or "primed," to withstand acute heat (Oliver and Palumbi, 2011; Palumbi et al., 2014; Ainsworth et al., 2016); the identity of the resident Symbiodiniaceae strongly modulates the thermal threshold, with heat-tolerant *Durusdinium* (formerly clade D) conferring resistance relative to more sensitive *Cladocopium*, and post-bleaching symbiont shuffling offering a further, if often transient, route to elevated tolerance (Berkelmans and van Oppen, 2006; LaJeunesse et al., 2018; Baker et al., 2008); and standing genetic variation in the coral host provides raw material for adaptation and for assisted-evolution interventions (van Oppen et al., 2015; Palumbi et al., 2014). A second, equally important source of heterogeneity is physical: coarse satellite

products average temperature over grid cells tens of kilometres across and therefore cannot resolve the internal waves, tidal pumping, and upwelling that cool some reefs, nor the heat retention of shallow, semi-enclosed lagoons that warm others (Reid et al., 2019; Wyatt et al., 2020, 2023; Safaie et al., 2018). High-frequency temperature variability, in particular, is among the strongest known correlates of reduced bleaching risk (Safaie et al., 2018).

The reefs that consistently bleach less than expected are of exceptional scientific and conservation value. They may function as thermal refugia or "bright spots" that harbour tolerant genotypes and symbiont assemblages, and they are prime targets for protection, for sourcing stock for restoration, and for mechanistic study (Cacciapaglia and van Woesik, 2021; Lachs et al., 2023; Schoepf et al., 2020). Encouragingly, community-level thermal tolerance can itself increase through time as recurrent heatwaves filter and acclimate assemblages, buying reefs additional decades under moderate-emissions trajectories (Lachs et al., 2023). Recent work has further proposed that equatorial reefs may experience systematically weaker heat stress than their higher-latitude counterparts, raising the possibility of a broad "equatorial refugia" zone (Ferris et al., 2025; Sully et al., 2019). Conversely, reefs that bleach far more than expected flag either uniquely vulnerable populations or, importantly, locations where the satellite record systematically underestimates the true in-water thermal dose — information that is itself valuable for improving stress forecasting.

Despite the clear value of such reefs, most bleaching analyses model the *average* relationship between heat and bleaching rather than the systematic deviations from it. Here we invert that emphasis. We build a predictive model of the expected bleaching response given the heat a reef actually experienced, and then treat the residual — the part of the response unexplained by measured heat exposure or by regional and inter-annual context — as the quantity of interest. By aggregating residuals across reefs that were surveyed repeatedly, we distinguish sites that deviate *consistently* from expectation (candidate resilient or sensitive reefs) from those that had a single unusual survey. Our objectives are threefold: (i) to assemble a reproducible, satellite-anchored measure of antecedent thermal stress for every survey in a global bleaching database; (ii) to rank repeatedly monitored reefs by their consistent over- or under-bleaching and deliver candidate lists of resilient and sensitive reefs with quantified uncertainty; and (iii) to articulate the mechanistic hypotheses that could explain the anomalies and to design an experimental programme — temperature loggers, symbiont profiling, and controlled heat-tolerance assays — capable of discriminating genuine biological tolerance from thermal-exposure measurement error.

2 Methods

2.1 Bleaching observations

Coral bleaching observations were drawn from the Global Coral Bleaching Database compiled by the U.S. National Centers for Environmental Information (NCEI accession 0228498, version 1.1) (van Woesik, Robert and Kratochwill, Chelsi, 2022). The database contains 33 244 georeferenced survey records spanning 1963–2021, each reporting the percentage of the surveyed coral assemblage that was bleached (`PERCENT_BLEACHED`) together with the survey date, latitude, longitude, depth where available, and a coarse biogeographic region label (`CORAL_REGIONS`). The distribution of bleaching severity is strongly right-skewed: across all records the mean bleaching was 14.1% while the median was 1.0%, reflecting the preponderance of surveys conducted outside of active heat-stress conditions. The geographic, temporal, and severity distributions of the raw database are summarised in Figures 1–4.

2.2 Reef clustering and repeat-survey selection

Because our inference rests on *repeated* observation of the same reef, we first resolved surveys to stable reef locations. Survey coordinates were clustered with the DBSCAN algorithm using a Haversine metric and a 1 km neighbourhood radius, grouping nearby surveys into reef "sites" (`SITE_ID`) while leaving isolated surveys ungrouped. We retained the 15 600 survey records belonging to sites that were visited on more than one occasion, yielding 1358 repeatedly monitored reef clusters with survey dates spanning 23 May 2002 to 6 September 2021. This repeat-survey subset is the analytical basis for all subsequent modelling and ranking.

2.3 Satellite temperature and antecedent thermal-stress metrics

Sea surface temperature (SST) was obtained from the NOAA Daily Optimum Interpolation SST analysis, version 2.1 (OISST v2.1), which provides daily, gap-free, 0.25° global fields from September 1981 to the present by blending in-situ ship, buoy, and Argo observations with satellite retrievals (Reynolds et al., 2007; Huang et al., 2021). For each reef cluster we extracted the daily SST time series of the containing 0.25° grid cell; 54 coastal cells that fell on masked (land) pixels were snapped to the nearest valid ocean cell. Across 670 grid cells the fraction of missing daily values was negligible (1.4×10^{-4}).

For every grid cell we constructed a daily climatology from the 1982–2011 baseline period, smoothing the day-of-year mean with a 15-day circular moving average to suppress sampling noise while preserving the seasonal cycle (Figure 5). The daily thermal anomaly is the observed SST minus this climatological expectation. For each survey we then summarised the anomalies over the half-open 84-day (12-week) window immediately preceding the survey, $[\,t_{\text{survey}} - 84\,\text{d},\ t_{\text{survey}})$, chosen to approximate the accumulation timescale over which heat stress drives bleaching while excluding the survey day itself. Three complementary exposure metrics were computed: the *cumulative positive anomaly* (the integral of positive anomalies, in °C-days), the *maximum anomaly* (the single hottest daily departure, in °C), and the *event duration* (the number of days with a positive anomaly). Over the repeat-survey set these averaged 50.0 °C-days, 1.52 °C, and 68.5 days respectively. This 84-day cumulative-anomaly construction is conceptually analogous to, but distinct from, the operational Degree Heating Week product of NOAA Coral Reef Watch (Liu et al., 2014; Skirving et al., 2020; Kayanne et al., 2017); we adopt an anomaly integral relative to a full 30-year daily climatology so that the metric is internally consistent across the entire global record.

2.4 Model of expected bleaching

The response variable — the proportion of the assemblage bleached — is a fraction bounded in $[0, 1]$ with substantial mass at the boundaries, so ordinary least squares and log-odds transforms are inappropriate. We therefore modelled `PERCENT_BLEACHED`/100 with a fractional logistic regression, i.e. a generalized linear model with a binomial family and a logit link fitted by quasi-maximum likelihood, following the fractional-response framework of Papke and Wooldridge (1996). The linear predictor comprised the three thermal-exposure metrics, each z-standardized to mean zero and unit variance, plus fixed effects for biogeographic region (`CORAL_REGIONS`; four levels) and survey year (18 levels) to absorb broad spatial baselines and the pronounced inter-annual structure of global bleaching. Of the 15 600 repeat-survey records, 12 296 carried a usable observed bleaching response and entered the fit (3304 lacked a response value). The model converged and achieved a McFadden pseudo-R^2 of 0.102 (Akaike information criterion 7758.3; log-likelihood −3855.1).

Because the three exposure metrics are physically correlated, we assessed multicollinearity

with variance inflation factors (VIF) and additionally fitted single-predictor models to recover the unconfounded marginal association of each metric with bleaching. The predictive skill of the full model on unseen reefs was evaluated by spatially blocked cross-validation: a leave-site-out scheme using `GroupKFold` with ten folds grouped by `SITE_ID`, so that all surveys of a given reef are held out together and no reef contributes to both training and test sets (Roberts et al., 2017; Hijmans, 2012). We report mean absolute error (MAE), root mean squared error (RMSE), and a predictive R^2 aggregated across folds.

2.5 Residuals, site-level ranking, and candidate selection

For each survey we computed the residual as the observed minus the model-expected percentage bleached; the survey-level residual standard deviation was 21.5%, which we use to define an approximate 95% prediction band ($\pm 1.96\times$ residual SD) around the 1:1 line. Residuals were then aggregated to the reef-site level: for each site we computed the mean residual, its standard error (residual standard deviation divided by $\sqrt{n}$, a measure of consistency across repeat visits), the number of surveys, mean observed and expected bleaching, and representative coordinates. Only sites with at least two observed surveys were ranked (1223 of the 1358 clusters), so that rankings reflect repeated anomalous behaviour rather than an isolated observation.

We applied a dual selection criterion designed to balance effect size against statistical confidence. First, an effect-size ranking selected the 30 sites with the most negative mean residual (candidate *resilient* reefs, which bleach less than their heat exposure predicts) and the 30 with the most positive mean residual (candidate *sensitive* reefs). Second, for every site we tested the per-site mean residual against zero with a one-sample t-test and corrected across all 1223 sites for multiple comparisons using the Benjamini–Hochberg false-discovery-rate (FDR) procedure at $q < 0.05$ (Benjamini and Hochberg, 1995). The resulting significance flag is carried in the candidate tables so that field teams can prioritise reefs that are both extreme and statistically consistent. All analyses used a fixed random seed for reproducibility.

3 Results

3.1 Structure of the global bleaching and temperature record

The repeat-survey subset spans all major reef provinces but is unevenly distributed, with dense sampling in the Caribbean/Gulf of Mexico, the Great Barrier Reef, and a broad "Other Reef" category encompassing the Indo-Pacific (Figure 1). The number of surveys per site is likewise skewed, with most reefs visited a handful of times and a minority monitored intensively (Figure 2); the temporal distribution concentrates after 2002, when standardized monitoring intensified (Figure 3). Bleaching severity is dominated by low values punctuated by a long tail of severe events (Figure 4). The smoothed 1982–2011 daily climatology captures the seasonal SST cycle cleanly and provides a stable baseline against which anomalies were measured (Figure 5).

3.2 Heat exposure predicts bleaching, with cumulative accumulation dominant

All three thermal-exposure metrics were positively associated with bleaching in single-predictor models: a one-standard-deviation increase raised the odds of bleaching by a factor of 1.91 for cumulative positive anomaly ($p \approx 10^{-104}$, pseudo-$R^2 = 0.096$), 2.00 for event duration ($p \approx 10^{-61}$), and 1.39 for maximum anomaly ($p \approx 10^{-31}$). In the full multivariable model, cumulative positive

anomaly emerged as the dominant predictor, with an odds ratio of 2.23 per standard deviation (95% CI 1.98–2.51; $p = 4.3 \times 10^{-39}$). Event duration retained a modest positive effect (odds ratio 1.12, $p = 0.046$), whereas the coefficient on maximum anomaly reversed to become weakly negative (odds ratio 0.75, $p = 5.6 \times 10^{-9}$). This sign reversal is a classic suppression artefact of collinearity: the three metrics are strongly intercorrelated (Pearson $r = 0.79$ between cumulative and maximum anomaly; $r = 0.76$ between cumulative anomaly and duration), and the variance inflation factor for cumulative anomaly reached 5.15. Once cumulative accumulation is in the model it absorbs the shared signal, so the residual partial effect of the peak temperature is not interpretable in isolation — the unconfounded single-predictor fits confirm that all three metrics are individually positive drivers of bleaching. Region and year fixed effects were highly significant, confirming that broad biogeographic and inter-annual baselines matter: relative to the reference region, the West-Indian, Great Barrier Reef, and Other Reef categories all showed significantly lower baseline bleaching odds. Figure 6 summarises the coefficient estimates, the observed-versus- predicted relationship, and the residual behaviour of the fitted model.

Crucially, the model generalized to reefs it had never seen. Under the leave-site-out cross-validation, in which every survey of a held-out reef was predicted from a model trained only on other reefs, the mean absolute error was 15.0% bleaching, the RMSE was 21.7%, and the predictive R^2 was 0.164, with consistent performance across all ten spatial folds (fold-level MAE 12.9–19.9%). The predictive skill is deliberately modest — bleaching is intrinsically noisy and much of its variance is local — but the fact that a heat-and-context model transfers to new reefs at all is what licenses the interpretation of large, consistent residuals as biologically or physically meaningful anomalies rather than overfitting.

3.3 Resilient and sensitive candidate reefs

Aggregating residuals across the 1223 repeatedly surveyed reefs produced an approximately symmetric site-level distribution (mean −0.25%, standard deviation 17.8%) with pronounced tails: 322 sites deviated significantly from zero after FDR correction. Ranking by mean residual yielded 30 resilient and 30 sensitive candidate reefs (Figure 7). The resilient short-list is defined by mean residuals at or below −21.3% and the sensitive short-list by mean residuals at or above +54.4%; of these, 11 resilient and 17 sensitive candidates remain significant after FDR correction, giving a high-confidence set of 28 reefs for priority fieldwork.

The two groups are geographically coherent in a way that provides an independent plausibility check on the method (Figure 8). Resilient candidates cluster markedly in the central-equatorial Pacific — the Phoenix and Line Islands of Kiribati around 2°–5° south and 170°–175° west — with additional sites scattered through the Caribbean and two on the Great Barrier Reef. By region, the resilient list comprises 17 “Other Reef” (predominantly equatorial Pacific), 11 Caribbean/Gulf of Mexico, and 2 Great Barrier Reef sites. The single most resilient reef, a Phoenix Islands cluster at approximately 2.8° S, 171.7° W, bleached on average only 11.6% despite antecedent heat that predicted 47.1% bleaching — a residual of −35.5%. This central-equatorial Pacific signal is consistent with the region’s vigorous equatorial upwelling and advective mixing, which supply cool water and high-frequency thermal variability that a 0.25° satellite average cannot capture (Reid et al., 2019; Safaie et al., 2018; Wyatt et al., 2020).

The sensitive candidates present a strikingly different and mechanistically informative pattern. The most extreme sensitive reefs form a tight cluster in the Ryukyu (Yaeyama) Islands of southern Japan, around 24.2° N and 124.0°–124.2° E. At the single most sensitive site (24.25° N, 124.11° E) the surveyed assemblage bleached completely (100%) while the satellite-derived heat exposure

predicted only 3.8% — a residual of +96.2%. Multiple neighbouring Ryukyu sites show the same signature of near-total observed bleaching against single-digit predicted values, and this cluster dominates the FDR-significant sensitive set. Such an extreme, spatially concentrated, and repeatable mismatch is the classic fingerprint of sub-grid thermal stress: the Yaeyama reefs sit in shallow, semi-enclosed lagoons with restricted circulation, where localised heat retention produces in-water temperatures well above the 0.25° open-ocean average (Wyatt et al., 2023; Kayanne et al., 2017). Overall the sensitive list comprises 14 Caribbean/Gulf of Mexico, 11 "Other Reef" (including the Ryukyu cluster), and 5 Great Barrier Reef sites. The observed-versus-expected relationship for all surveys, with candidates highlighted and the 95% prediction band shown, is given in Figure 7; the geographic distribution of candidates coloured by mean residual is shown in Figure 8. The complete ranked list of all 1223 sites, together with the two 30-reef candidate tables, accompanies this paper as supplementary data.

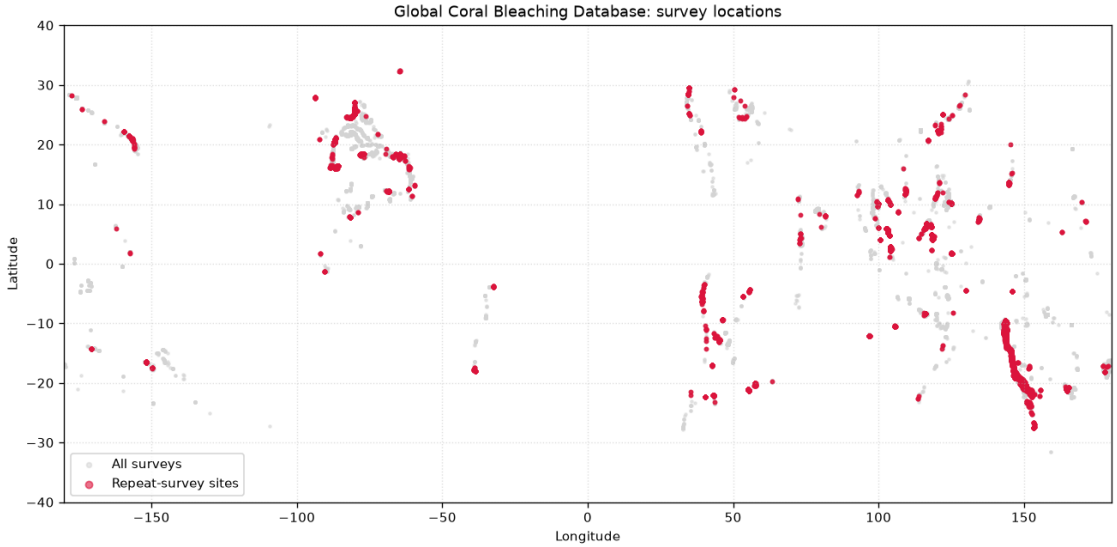

Figure 1: Geographic distribution of coral bleaching surveys in the repeat-survey subset of the Global Coral Bleaching Database, coloured by biogeographic region. Sampling is dense in the Caribbean/Gulf of Mexico and the Great Barrier Reef and broadly distributed across the Indo-Pacific "Other Reef" province.

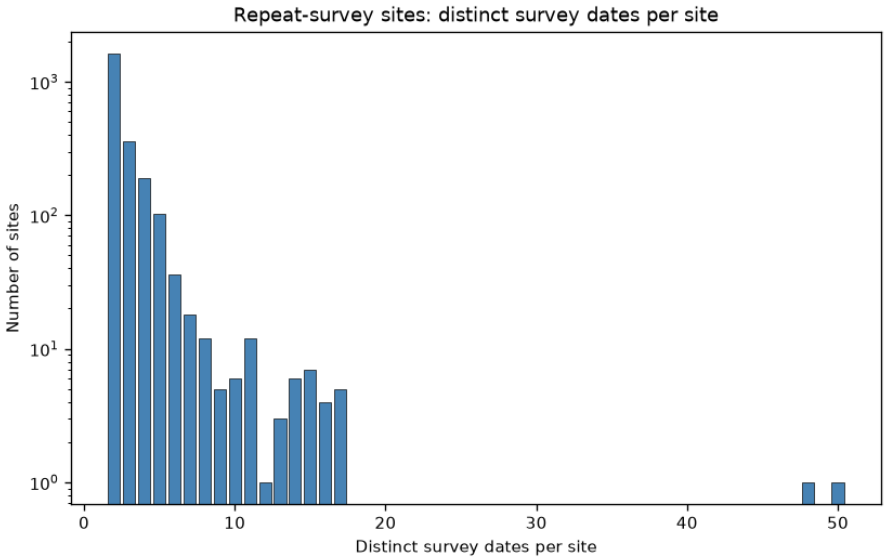

Figure 2: Distribution of the number of surveys per reef site after DBSCAN (1 km) clustering. Most reefs were visited a small number of times, while a minority were monitored intensively; only sites with ≥ 2 surveys enter the candidate ranking.

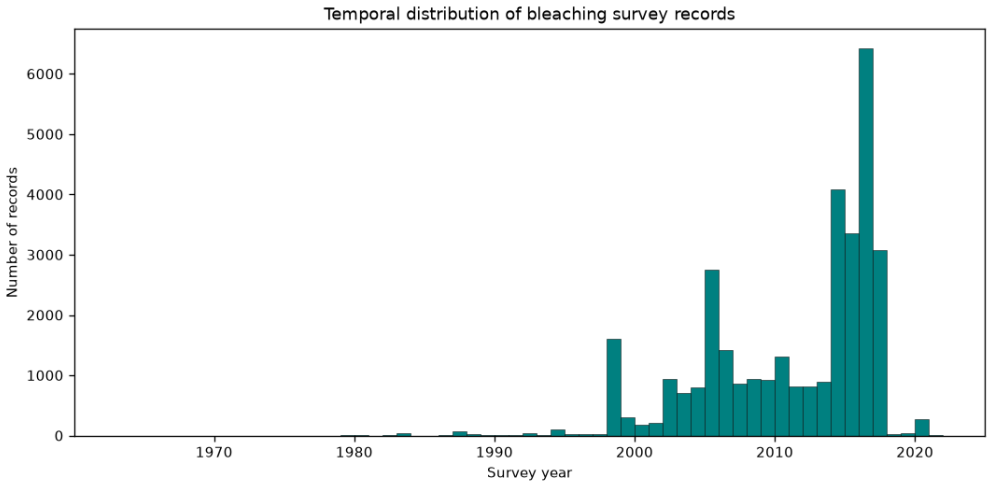

Figure 3: Temporal distribution of surveys. Standardized monitoring intensifies after 2002, the period on which the modelling is concentrated.

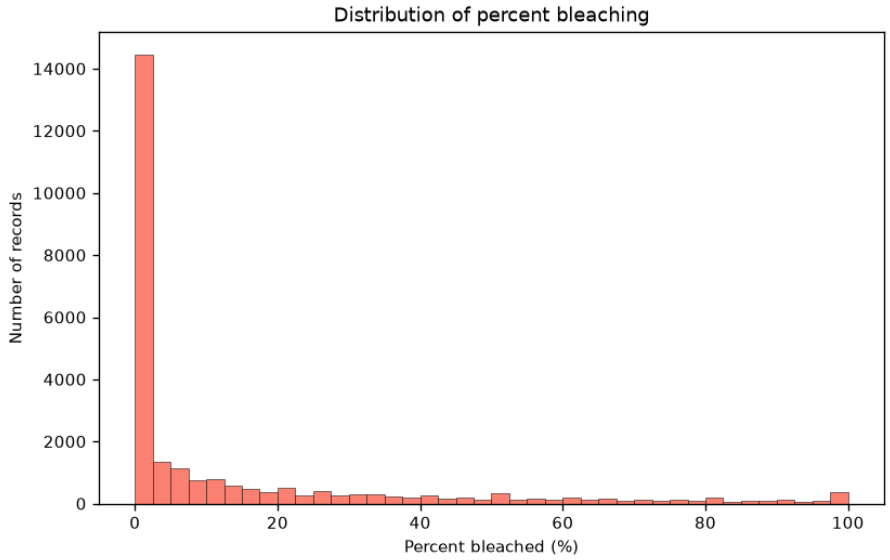

Figure 4: Distribution of the response variable, the percentage of the surveyed assemblage bleached. The distribution is strongly right-skewed (median 1.0%, mean 14.1%), motivating a fractional logistic model.

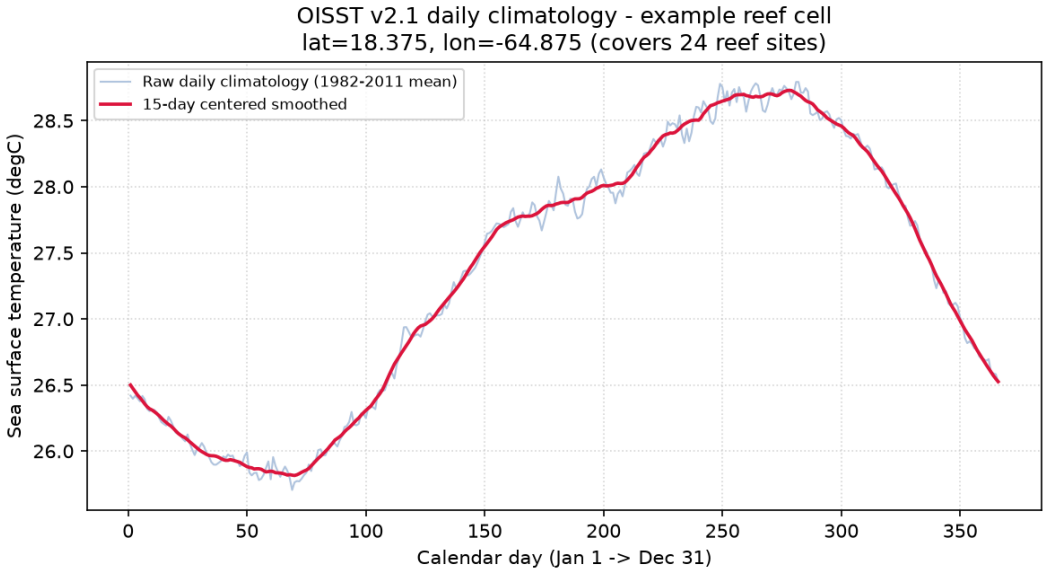

Figure 5: Example OISST daily climatology for a single 0.25° grid cell. The 15-day circular-smoothed 1982–2011 day-of-year mean (baseline) is overlaid on the observed daily SST; positive departures above the baseline within the 84-day pre-survey window define the thermal-exposure metrics.

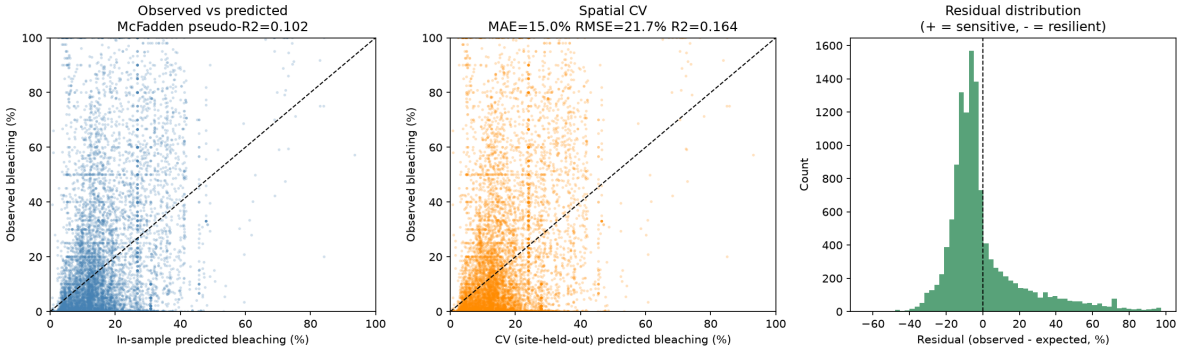

Figure 6: Diagnostics for the fractional logistic model of expected bleaching: standardized coefficient estimates for the thermal-exposure metrics and fixed effects, the observed-versus-predicted relationship, and residual behaviour. Cumulative positive anomaly is the dominant predictor.

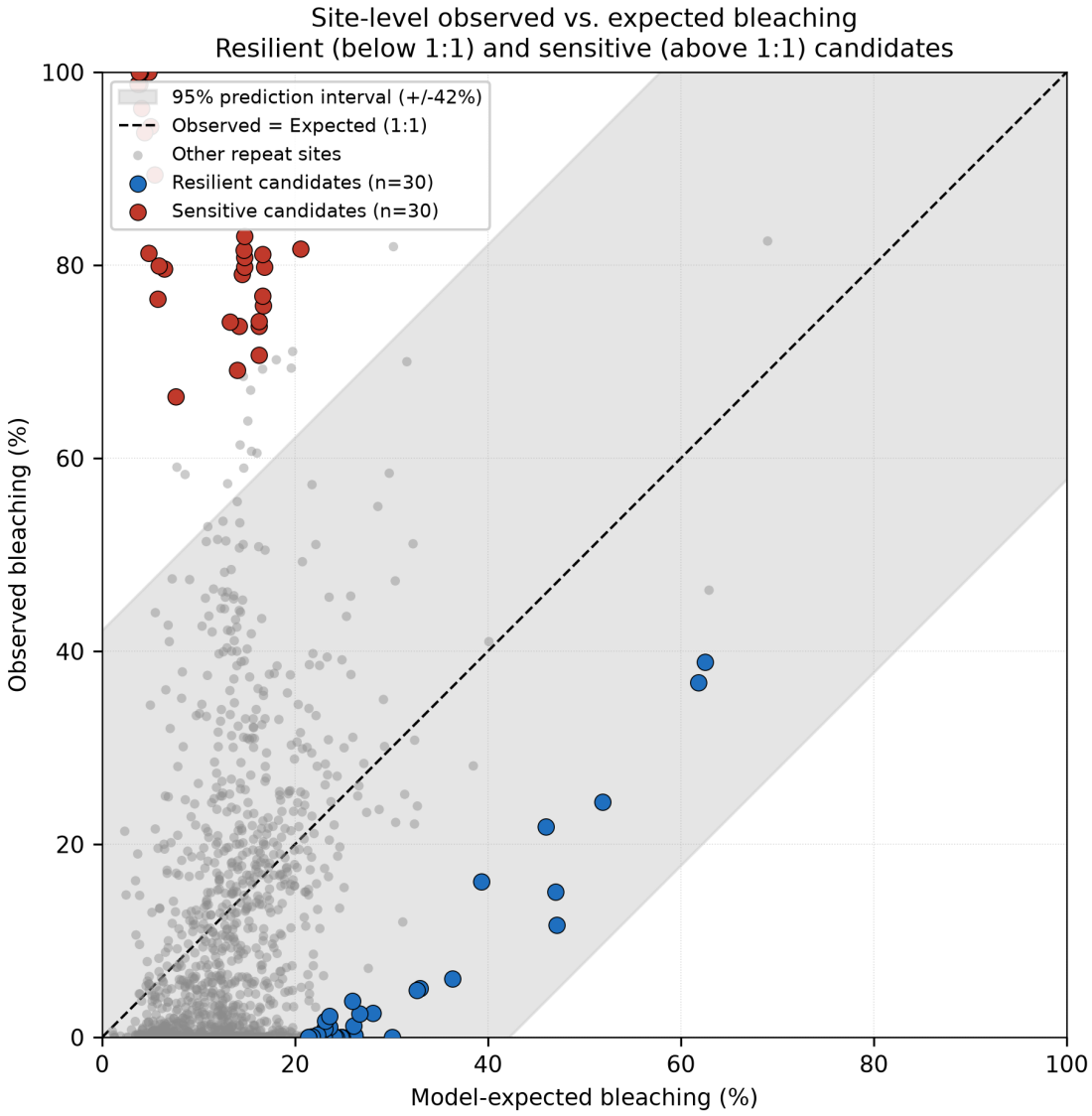

Figure 7: Observed versus model-expected percentage bleached for all surveys. The 1:1 line marks perfect prediction and the shaded band shows the approximate 95% prediction interval (±1.96× residual standard deviation). Resilient candidates (large negative residual; below the band) and sensitive candidates (large positive residual; above the band) are highlighted. The extreme sensitive points at the upper-left — near-total observed bleaching against near-zero predicted bleaching — are the Ryukyu lagoon cluster.

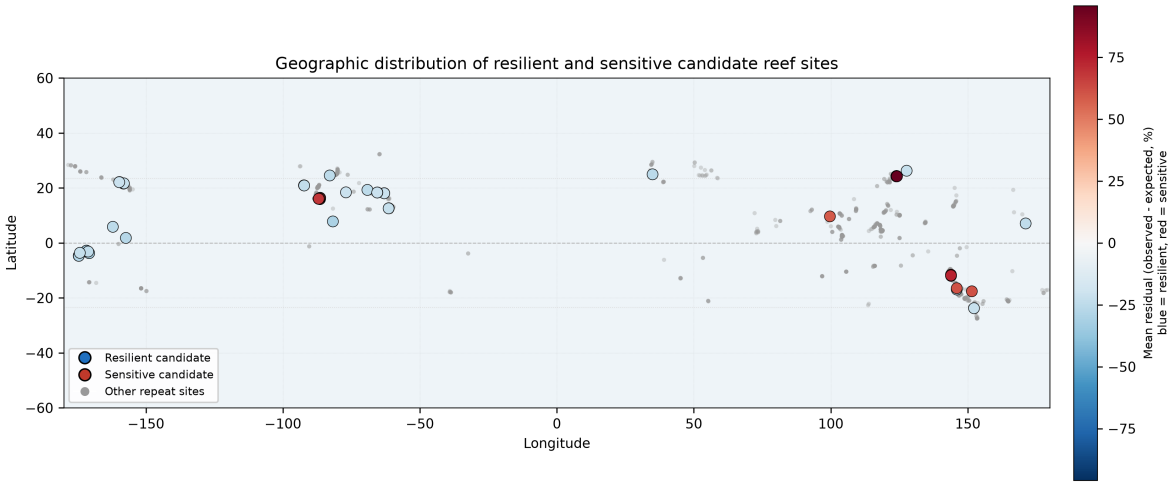

Figure 8: Global distribution of candidate reefs coloured by mean site-level residual. Resilient reefs (blue/green; bleach less than expected) cluster in the central-equatorial Pacific, while the most extreme sensitive reefs (red; bleach more than expected) cluster in the Ryukyu Islands of southern Japan. Equator and tropic guide lines are shown.

4 Discussion

Framing coral bleaching in terms of the residual from a heat-and-context model shifts attention from the well-established average response to the reefs that most defy it, and it does so on a global, reproducible, satellite-anchored footing. Our model recovers the expected physiology: cumulative heat accumulation over the preceding season is the strongest single correlate of bleaching, more informative than the peak temperature alone, echoing both the mechanistic understanding that bleaching is a dose-dependent process and the operational success of accumulation-based indices such as Degree Heating Weeks (Liu et al., 2014; Skirving et al., 2020; Eakin et al., 2019; Rädecker et al., 2021). That the model transfers to spatially held-out reefs with a mean absolute error near 15% gives us confidence that large, repeatable residuals are signal rather than noise. The two candidate groups that emerge are not statistical curiosities: they fall into biogeographically coherent clusters whose geography points directly at competing mechanisms.

The central-equatorial Pacific clustering of resilient reefs is the more encouraging finding. Reefs of the Phoenix and Line Islands repeatedly bleached far less than their satellite heat exposure implied. Two non-exclusive explanations are consistent with this pattern. The first is physical: this region is characterised by equatorial upwelling, strong zonal currents, and internal-wave activity that inject cool water and impose large high-frequency temperature fluctuations, all of which are missed by a 0.25° daily average yet are among the most powerful known suppressors of bleaching risk (Safaie et al., 2018; Reid et al., 2019; Wyatt et al., 2020). The second is biological: reefs subjected to chronically variable temperatures are repeatedly pre-conditioned, and such thermal priming can elevate bleaching thresholds through symbiont and host acclimatization (Oliver and Palumbi, 2011; Palumbi et al., 2014; Ainsworth et al., 2016). These interpretations connect to the broader debate over whether equatorial reefs constitute a systematic refugium: recent analyses argue that bleaching is often weaker near the Equator than at tropical mid-latitudes, though the eastern and central Pacific are noted as regionally variable (Ferris et al., 2025; Sully et al., 2019). Our residual-based identification of Kiribati reefs as consistent over-performers is congruent with, and adds site-level specificity to, that emerging picture, and it identifies concrete targets for the kind of long-term

tolerance monitoring that has revealed emergent increases in thermal tolerance elsewhere in the Pacific (Lachs et al., 2023).

The Ryukyu/Yaeyama clustering of the most extreme sensitive reefs carries a different and cautionary message. When a reef bleaches completely while the satellite record reports almost no anomaly, the most parsimonious explanation is not that the corals are uniquely fragile but that the thermometer is in the wrong place. The Yaeyama sites occupy shallow, semi-enclosed lagoons where restricted circulation permits pronounced local heat build-up that a coarse open-ocean product cannot resolve (Wyatt et al., 2023; Kayanne et al., 2017). This interpretation reframes the most dramatic residuals in our analysis as a diagnosis of sub-grid thermal stress — an exposure-measurement error — rather than of biological hypersensitivity, and it underscores a general limitation of satellite-only bleaching forecasting in geographically complex, nearshore reef systems. Distinguishing these two possibilities is not merely academic: a reef that is genuinely hypersensitive warrants triage and assisted-evolution attention, whereas a reef whose apparent sensitivity is an artefact of unresolved heating instead calls for improved in-situ monitoring and locally corrected heat-stress products.

These competing explanations motivate an explicit validation programme, because the residual by construction absorbs every process the model omits — unresolved temperature, differences in species composition between surveys, local water quality, and observation error — and cannot by itself attribute an anomaly to a mechanism. We therefore frame five non-exclusive hypotheses and a field design to discriminate among them. Hypothesis H1 (local hydrodynamic cooling of resilient reefs, or heat trapping at sensitive lagoon reefs) is an exposure-measurement hypothesis; hypotheses H2–H5 (thermal priming, symbiont community composition, depth/light refugia, and standing genetic adaptation) concern genuine holobiont tolerance. The pivotal experiment is the deployment of high-frequency in-situ temperature loggers (Onset HOBO U22-001 or TidbiT MX2203, accuracy $\pm 0.2\,^{\circ}\mathrm{C}$, logging every 10–15 minutes) at the survey depth, complemented by shallow and deep loggers at a subset of sites to probe vertical structure. Recomputing our 84-day anomaly metrics from the in-situ series against the same 1982–2011 baseline provides a clean decision rule: if a candidate's residual collapses toward zero once in-water stress is substituted for satellite stress, the anomaly was primarily an exposure artefact (H1) — the expected outcome for the Ryukyu cluster; if a substantial residual persists, the deviation reflects intrinsic tolerance and warrants biological dissection.

That biological dissection rests on two established assays. Symbiont community composition is characterised by ITS2 metabarcoding analysed through the SymPortal framework, with quantitative PCR as a confirmatory measure of low-abundance background symbionts (Hume et al., 2019; LaJeunesse et al., 2018). The prediction is explicit: resilient reefs should be enriched in heat-tolerant *Durusdinium*, while sensitive reefs should be dominated by thermally susceptible *Cladocopium* (Berkelmans and van Oppen, 2006; Voolstra et al., 2020). Repeat sampling before and after a warm season additionally tests for active symbiont shuffling. Intrinsic thermal tolerance is then measured directly and comparably using the Coral Bleaching Automated Stress System (CBASS), a portable flow-through platform that delivers a standardized acute thermal ramp across four treatments (local maximum monthly mean and +3, +6, $+9\,^{\circ}\mathrm{C}$) and yields a dose–response thermal threshold (ED50) from photochemical yield ($F_{\mathrm{v}}/F_{\mathrm{m}}$) measurements (Evensen et al., 2023; Voolstra et al., 2020). Because CBASS holds all colonies under identical conditions, a higher ED50 in resilient candidates constitutes direct evidence of tolerance that is independent of in-situ exposure; pairing the assay with host genotyping partitions the host and symbiont contributions and tests for the standing genetic variation that underpins assisted-evolution strategies (van Oppen et al., 2015; Palumbi et al., 2014). A candidate is regarded as validated only when at least one biological line of evidence

confirms the direction of its anomaly *after* exposure error has been accounted for.

Several limitations temper these conclusions. The predictive skill of the model is modest by design, and much of the survey-to-survey variance in bleaching is local and unmodelled; we mitigate over-interpretation by requiring anomalies to be consistent across repeat visits and by reporting FDR significance. Many candidates rest on only two to four surveys, so the high-confidence subset flagged by the FDR procedure should be prioritised for fieldwork, and matched resilient–sensitive pairs should be sampled within a region to avoid confounding tolerance with biogeography. The bleaching database itself aggregates surveys conducted with heterogeneous methods and taxonomic resolution, and standardization of in-situ bleaching measurement remains an active challenge for the field (McClanahan et al., 2020). Finally, and most importantly, our residual metric cannot distinguish exposure error from biology on its own — which is precisely why the experimental programme is an integral part of the study rather than an afterthought. Notwithstanding these caveats, the approach delivers a ranked, uncertainty- quantified, and mechanistically interpretable global short-list of reefs that most defy their thermal environment, providing an actionable bridge between large-scale observational synthesis and targeted physiological validation at a time when the window for coral persistence is narrowing (Hughes et al., 2018b; Lachs et al., 2023; van Woesik et al., 2022).

5 Conclusion

By modelling the expected bleaching response to antecedent heat and studying the residuals, we converted four decades of global bleaching and satellite temperature records into a concrete, prioritised set of resilient and sensitive candidate reefs. Cumulative seasonal heat accumulation is the dominant driver of bleaching, and a heat-and-context model that transfers to unseen reefs provides a principled baseline against which anomalies can be judged. The resilient candidates concentrate in the central-equatorial Pacific, consistent with hydrodynamic cooling and thermal priming and with the emerging notion of equatorial refugia; the most extreme sensitive candidates concentrate in the semi-enclosed lagoons of the Ryukyu Islands, where they most plausibly signal sub-grid thermal stress invisible to satellites. We deliver the ranked candidate lists together with an integrated validation programme — in-situ loggers, ITS2 symbiont profiling, and CBASS heat-tolerance assays — explicitly constructed to separate genuine holobiont tolerance from thermal-exposure measurement error. Applied to the high-confidence candidates, this programme would convert statistical anomalies into mechanistically validated conservation targets and improve the thermal-stress products on which reef management increasingly depends.

Data and code availability

The bleaching observations are from the Global Coral Bleaching Database, NCEI accession 0228498 v1.1 (van Woesik, Robert and Kratochwill, Chelsi, 2022). Sea surface temperatures are from NOAA OISST v2.1 (Huang et al., 2021). Ranked site tables and candidate lists accompany this manuscript as supplementary data.

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