

Machine-learning and prioritization models reveal climate refugia for coral reefs into 2050

Kyle J. A. Zawada¹, Emily S. Darling^{2*}, Stacy D. Jupiter², Timothy R. McClanahan², Joseph M. Maina¹

¹ School of Natural Sciences, Macquarie University, Sydney, Australia.

² Marine Program, Wildlife Conservation Society, Bronx, NY, USA.

* Corresponding author: edarling@wcs.org

Abstract

Climate change is accelerating the decline of coral reefs, yet some locations may retain conditions that support persistence under future warming. We compiled 45,064 coral field observations from 1960–2025 and 42 climate, biophysical, and human-pressure predictors to train machine-learning ensembles estimating coral cover and community composition in 2020 and 2050. Predictions span a global 250 m-resolution map of potential coral reef extent: 8.8 million pixels covering 552,969 km². Model performance varied by province and reflected field-data availability; predictions were restricted to regions where models passed pre-specified accuracy thresholds. We then used a multi-objective optimization framework to identify reef areas that jointly maximize current and future coral cover, community composition, spatial cohesion, and model certainty. Our results reveal 165,922 km² of potentially climate-resilient reef locations spanning 71 countries and 100 territories and jurisdictions, adding 30 countries and 54 jurisdictions beyond the original 50 Reefs assessment (Beyer et al 2018). More than half of this resilient habitat (61%; 100,755 km²) occurs within five countries with extensive reef systems: the Bahamas, Cuba, Australia, Indonesia, and the Philippines. These findings highlight the uneven but widespread global distribution of large-scale refugia and emphasize the opportunity for global efforts and countries to strategically focus policies, conservation finance, and management actions most likely to sustain coral reef futures.

Introduction

Coral reef ecosystems are experiencing unprecedented stress from increasingly frequent and severe marine heatwaves, driving widespread bleaching and mortality (Hughes et al 2017; Li and Donner 2022). These events have caused major losses in living coral cover (Hoegh-Guldberg et al 2023), reorganization of reef communities (Hughes et al 2017), and declines in ecological functioning (Pratchett et al 2011). Recent global bleaching has exposed an estimated 68–84% of shallow tropical reefs to bleaching-level heat stress, highlighting rapidly shifting climate baselines (Spady et al 2026). Consequently, climate threats indicate widespread degradation under future warming scenarios (Frieler et al 2013; Cornwall et al 2021; Zeng et al 2025) but require projections with finer spatial and temporal resolution to potentially evaluate the many factors shown to influence their persistence (McClanahan et al 2024a, McClanahan 2025). Coral reef forecasts indicate projections vary with the inclusion of

variables, training data, model structures, and taxa used to make predictions (Klein et al 2024; McClanahan 2025).

Growing tension between global heat stress and risk projections and observed local persistence has elevated the importance of local environmental factors and climate refugia in ecosystem and coral reef conservation. Evolutionary and ecological refugia are habitats where biodiversity can persist and potentially recover and expand after climatic threats have declined (Keppel et al 2012). Early work in coral reefs focused on conditions where corals avoid bleaching, such as areas with hydrodynamic cooling (Nakamura et al 2005; Schmidt et al 2016) and reduced solar irradiance from clouds or turbidity (Gonzalez-Espinosa and Donner 2021; Morais et al 2026; Sully and Van Woesik 2020). Recently, considerations of climate refugia have expanded to include not only areas that avoid climate stress, but also areas that can resist and recover, defined as an avoidance, resistance, recovery (ARR) framework of refugia (McClanahan et al 2024b).

Global efforts to map coral reef climate refugia have primarily focused on identifying areas that avoid acute thermal and cyclone stress. A major advance was the '50 Reefs', which optimized the selection of large reef areas (500 km²) projected to experience lower thermal stress and storm damage while maintaining strong larval connectivity (Beyer et al 2018; Hoegh-Guldberg et al 2018). This analysis has since guided more than US\$100 million in conservation investments (Bloomberg Philanthropies 2021). However, environmental datasets available in 2018 were relatively coarse (5 km or 0.05° resolution, ~31 km²) and the analysis did not integrate modifying variables such as oceanography or human pressures, factors known to strongly mediate local bleaching, coral mortality, and persistence (Loya et al 2001; Darling et al 2019; MacNeil et al 2019; McClanahan et al 2020; McClanahan 2023, 2025). In addition, Beyer et al (2018) did not incorporate empirical observations of coral cover or composition, nor training and testing data or predictive fits, limiting their ability to characterize the ecological responses that underpin the resilience of potential refugia. These limitations highlight the need for updated, higher-resolution assessments that incorporate a broader suite of ecological and environmental drivers and predictive modelling methods to identify fine-scale climate refugia.

Mapping the next generation of global reef refugia requires empirical measures of coral condition, including total coral cover and community composition, to better assess the mechanisms and probabilities that shape persistence. Total percent live coral cover is a composite metric aggregating many scleractinian coral taxa whose relative abundance influences the outcomes of heat and other climate change threats. Nevertheless, coral cover is the most frequently measured variable to assess reef status and likely reflects cumulative impacts, resistance, and recovery potential that supports key ecological functions and services (Perry et al 2013; Beck et al 2022). Community composition captures functional differences influencing adaptation, resistance, and recovery. Pooling taxa into competitive, stress-tolerant, and weedy life-history categories provides a useful framework for interpreting resilience (Darling et al 2012; Darling et al 2013). Dominance by large branching and plating competitive corals can indicate avoidance refugia; stress-tolerant assemblages of massive corals often signal resistance; and communities dominated by fast-growing weedy taxa typically support rapid recovery. These life-history strategies help identify three climate-refugia types: avoidance,

resistance, and recovery (ARR; McClanahan et al 2024b). While observations to coral genera are less commonly recorded than total coral cover, modelling coral life histories is investigated for its potential to provide a foundation for identifying ARR refugia.

Here, we aim to identify contemporary and future climate refugia for coral reefs using machine learning and multi-objective prioritization that combines empirical coral cover and community observations with environmental datasets and spatial optimization. Our framework also leverages high-resolution reef extent maps (e.g., Lyons et al 2024) and incorporates model uncertainty to identify locations for coral resilience on a 250 m grid, providing critical information to complement local knowledge and decision-making to ensure the persistence of ecological services to tropical reef stakeholders. Our goals are to: (1) model the current and future environmental conditions that influence coral cover and community composition; (2) prioritize climate refugia using multi-objective optimization and an ARR resilience framework; and (3) evaluate outcomes across global, regional, and national scales to inform conservation decision-making.

Methods

The workflow is summarized in Figure 1.

Empirical observations and predictor variables

We compiled a global dataset of coral reef ecological surveys conducted between 1960 and 2025 including 37,689 unique observations of total coral cover, of which 7,375 observations include coral genera abundance that, based on traits, have been classified into competitive, weedy, and stress-tolerant life-history groups (Fig. S1). Surveys were drawn from long-term monitoring programs, academic and government studies, published datasets, and other publicly available sources (Table S1). Observations were retained only if they fell within mapped reef extent from the Allen Coral Atlas (2022; <https://allencoralatlas.org/>) or the UNEP-WCMC Global Distribution of Coral Reefs (UNEP-WCMC et al 2021). Coral community composition was assigned by dominant life-history category (Table S2; Darling et al 2012, 2019) and its relationship to avoidance, resistance, and recovery refugia (ARR, McClanahan et al 2024b). We removed observations when essential predictors were missing; depth was the most frequently absent predictor and could not be reliably imputed in shallow, complex coastal settings with coarse scale predictions.

Environmental and anthropogenic predictors included 42 variables representing ocean temperature, chemistry, geomorphology, connectivity, and human pressure (see Supporting Information; Table S3). Sea surface temperature (SST) metrics captured both central tendencies and variability, including chronic long-term climatologies and 6-year windows preceding each survey year to represent background conditions and recent disturbances (McClanahan et al 2019). Additional predictors described chemistry (e.g. calcite, nutrients, dissolved oxygen, pH), light availability (PAR, Kd, benthic light), and modifying variables (e.g., depth, slope, ruggedness, geomorphic zones). These data combined static layers (e.g. human gravity, sediment plumes, connectivity) and time-varying layers derived from a diversity of

sources and spatial resolutions (Table S3). All environmental and anthropogenic predictors were spatially matched to surveys by extracting raster values at the latitude and longitude of each survey site; where time-varying layers were used, values were drawn from the annual or 6-year time window preceding the survey year.

Our modelling framework extends the global climate-refugia assessment of Beyer et al (2018) by explicitly incorporating empirical coral cover and community composition, a broader suite of environmental domains, and cross-validated model evaluation. Whereas the original 50 Reefs analysis focused primarily on excess heat, cyclone exposure, and larval connectivity, we integrate these drivers alongside a broader set of climate, oceanographic, and human pressure predictors with documented links to coral assemblages (e.g. McClanahan and Azali 2021; Table S3). By directly training machine learning models for total coral cover and life history abundance with these variables, we improve the ecological realism and spatial resolution of climate refugia predictions based on the direct modelling of present and future coral cover and composition.

Model development and training

All predictors were harmonized to a global 250 m x 250 m reef grid created by rasterizing and combining the 5 m-resolution Allen Coral Atlas and UNEP-WCMC vector reef extent datasets. The resulting mask comprised 8,847,504 reef pixels (552,969 km²). Resampling introduced minor boundary deviations, especially along sharp coastlines and environmental gradients, but ensured that all predictors were aligned at a common resolution. Coarse predictors were not downsampled, as interpolation would introduce spurious precision without adding information. Predictions are reported on a 250 m grid, but effective resolution is set by the coarsest input layer, producing visible artefacts where coarse predictors are clipped to fine-resolution boundaries or where grids are misaligned (Fig. S2; Table S3). Predictors were screened for multicollinearity using variance inflation factors ($VIF < 7$), yielding non-collinear feature sets for model training.

We modelled total hard coral cover and the cover of competitive, weedy, and stress-tolerant life histories using XGBoost gradient tree boosting (Chen and Guestrin 2016). Coral province was included as a categorical predictor to capture broad biogeographic structure (Keith et al 2013). To reduce spatial and temporal autocorrelation, surveys were grouped into spatiotemporal bins of ~11 km and five years. Bins were randomly assigned to training (50%), validation (25%), or testing (25%) sets using a three-way holdout (Raschka 2018). This procedure was repeated independently for 100 model runs per response variable ($n = 4$ responses). Models were trained with early stopping based on validation error, and hyperparameters were tuned within constrained ranges for tree depth, learning rate, subsampling, and regularization. In total, 400 gradient-boosting models (100 per response) were trained to quantify predictive robustness and variability.

Identifying drivers of coral cover and composition

We interpreted variable importance and effect direction using Shapley Additive Explanations

(SHAP; Lundberg et al 2019), which decompose model predictions into additive contributions from individual predictors while accounting for interactions and correlated features. For each model, we computed mean absolute SHAP values to summarize variable influence and examined SHAP–predictor correlations to determine effect direction. Conditional SHAP dependence plots were used to visualize nonlinear and threshold relationships while conditioning on the remaining predictors. Ensemble SHAP patterns were then used to characterise global drivers of total coral cover and community composition.

Model performance assessment and prediction

For each response variable, model performance was evaluated against a mean-only null model across 100 runs, using mean absolute error (MAE) and median absolute deviation (MAD). We defined skill as the proportional reduction in MAE or MAD relative to the null and required at least 10% improvement for a model to be retained. Paired permutation tests by coral province assessed whether skill exceeded this threshold. Only models meeting these criteria contributed to spatial predictions, allowing model sets to differ among provinces. Final ensembles were used to predict coral cover and life-history cover for all reef cells globally at 250 m grid for 2020, and coral cover in 2050. Future predictions used CMIP6 SSP3-7.0 forcing, a moderate mid-century emissions scenario (Eyring et al 2016). We selected SSP3-7.0 as the primary scenario because (i) it has emerged as a standard reference in recent coral reef projection studies (e.g. Kalmus et al 2022; DeCarlo et al 2025; Mellin et al 2025), and (ii) it sits within the plausible upper range of 21st-century emissions outcomes following the community's reassessment of SSP5-8.5 as implausibly high (Hausfather 2025; Van Vuuren et al 2026). For comparison and continuity with prior coral reef projection literature, results under SSP5-8.5 are presented in the Supporting Information.

Spatial optimization of climate refugia

For spatial optimization, we aggregated 250 m predictions to 5 km² (2.24 km × 2.24 km) planning units. Reef prioritisation was formulated as a binary integer linear program under a fixed 30% area budget applied independently per marine ecoregion (Spalding et al 2007), consistent with Kunming–Montreal Global Biodiversity Framework Target 3 (CBD 2022). Drawing on portfolio theory (Markowitz 1952), the model jointly optimizes four complementary objectives (equations in Appendix 1; see also Supporting Information): (i) a blended measure of present (2020) and projected future (2050) coral cover, weighted 0.7:0.3 to prioritize existing biological capital while addressing expected persistence; (ii) spatial cohesion, rewarding compact, connected reef networks via a k-nearest-neighbour metric with distance-decay weighting; (iii) representation across coral life-history strategies (competitive, stress-tolerant, weedy), with a square-root transformation to introduce diminishing returns and optional ecoregion-level rarity weighting; and (iv) risk minimization, penalizing reefs with high predictive uncertainty across 100 ensemble runs and projected coral cover declines between 2020 and 2050. Optimisations were solved using the Gurobi Optimizer (Gurobi Optimization LLC 2026) with lexicographic multi-objective settings. Prioritised reef pixels were intersected with Exclusive Economic Zones and protected area polygons (UNEP-WCMC and IUCN 2026) and compared with the Beyer et al (2018) portfolio.

Results and Discussion

Mapped potential coral reef extent

After combining two global coral reef habitat maps (Allen Coral Atlas 2022; UNEP-WCMC et al 2021) at 250 m grid resolution, we identified 552,969 km² of coral habitat for assessment of climate resilience characteristics. This estimate is substantially greater than recent satellite-derived values of 348,361 km² (Lyons et al 2024, Allen Coral Atlas 2022), 249,713 km² (Burke et al 2011), and 284,300 km² (UNEP-WCMC et al 2021), but closer to an earlier environmentally-derived estimate of ~600,000 km² (ReefBase 1996 *sensu* Kleypas et al 1999), suggesting that environmental approaches tend to yield larger areas than satellite-based detection. Differences likely reflect a combination of input-layer resolution, depth limits in satellite mapping (e.g., 15 m in Lyons et al 2024), and our aggregation approach (see Supplementary Methods). We treated the combined map as potential coral reef extent, i.e., the spatial envelope where reef habitat could plausibly occur, rather than as a map of currently occupied reefs. Distinguishing potential from realized habitat will nonetheless require further groundtruthing (e.g., Andréfouët et al 2024).

Predictive modelling and performance

Globally and across responses, independent testing R^2 ranged from 0.08–0.28, and MAE from 3–13%, with low variation across the 100-run ensemble indicating stable results (Table S4). At the global scale, total coral cover had the highest predictive R^2 (0.28) and, in absolute terms, the largest MAE (12.9%; Table S4), although this partly reflects its wider response range (0 to ~80%) relative to the life-history groups (e.g., 0 to ~20% for weedy taxa); proportionally, total coral cover error is on par with or lower than the life-history models.

Machine-learning models for total coral cover and for the cover of competitive, stress-tolerant, and weedy life histories showed marked differences among provinces (Fig. S3). The Africa-India, Indonesian, Atlantic Caribbean, and Hawaii-Line Islands provinces had the highest proportion of total coral cover models meeting skill thresholds (Table S5), likely reflecting more field observations available for training. Overall, ≥75% of coral cover models passed both skill thresholds (≥10% reduction in mean error and error variance relative to the null) in 9 of 14 provinces (Table S5). Among life histories, stress-tolerant models most often passed thresholds, followed by competitive and then weedy models (Tables S4, S5). Only competitive corals in the Persian Gulf failed to produce any models above the skill threshold (1 of 52 province x life-history combinations); predictions for this combination were not generated, and competitive coral cover in the Persian Gulf was excluded from subsequent prioritization. Variation in model skill across provinces likely reflects limitations in training data availability; expanded access to monitoring data would improve future predictions.

Drivers of coral cover and composition

SHAP summaries and partial dependence plots (Fig. 2, Fig. S4) highlighted consistent predictors of coral cover, including temperature variability and extreme heat, distance from 500 m depth, light, cyclone maximum wind speed, and connectivity. Coral cover declined with increasing SST variability (SD, skewness), acute extreme heat (6-year DHW), maximum cyclone strength and light, and increased with extreme heat (SST 0.9 quantile), distance from 500 m depth, and connectivity. Non-linear responses were common (Fig. S4). These same predictors structured trait-specific responses across coral life histories (Fig. 2), though with weaker overall model fits: competitive corals declined with human gravity (a fishing pressure proxy; Cinner et al 2018), depth, and temperature; weedy corals showed opportunistic positive responses to human gravity, cyclones, light, sedimentation, and SST metrics (Darling et al 2012, 2013; Zinke et al 2018); and stress-tolerant corals declined under most environmental stressors but increased under extreme heat (SST 0.9 quantile), consistent with their replacement of more sensitive taxa after repeated bleaching (Darling et al 2019; McClanahan et al 2020).

Spatial prioritization of climate refugia and implications for conservation

Our spatial optimization yielded a globally distributed portfolio of climate-resilient reef areas (Fig. 3). The optimization drew on 2020 predictions of coral cover and community composition and 2050 coral cover predictions under SSP3-7.0 (a moderate mid-century emissions scenario); community composition was not projected to 2050 because life-history models showed lower and more variable skill across provinces (Table S5). Selected sites scored higher across all portfolio objectives (Fig. 4), and z-score maps show how objective variability shaped outcomes (Fig. S5). The full 250 m global prioritization surface underlying the portfolio analysis is publicly available as a GeoTIFF (Zawada et al 2026) corresponding to the optimized solution (<https://doi.org/10.5281/zenodo.18686274>). A portfolio analysis under a high emissions SSP5-8.5 scenario is presented in Figs. S6-S8 and Table S7.

From the 552,969 km² of mapped potential coral reef extent, the prioritization identified 165,922 km² of climate-resilient reefs across 71 countries and 100 territories and jurisdictions (Fig. 5; Table S6). This expands on Beyer et al (2018), whose portfolio covered 147,284 km² across 41 countries and 46 territories and jurisdictions. Only 37,576 km² overlapped between the two analyses, indicating an expansion of identified climate-resilient reef area relative to Beyer et al (2018), referred to here as the '50 Reefs plus' portfolio. We note that differences between the two portfolios reflect both the broader suite of predictors and updated data used here and the uncertainty inherent in the underlying machine learning models; the non-overlapping areas should be interpreted as candidate priorities for further evaluation (Table S6, see also Table S7).

More than half of the new priority areas (100,755 km², or 60.3%) occur in five countries: the Bahamas (32,105 km² out of 106,542 km², or 30.1%), Cuba (18,914 km² out of 54,298 km², 34.8%), Australia (18,390 km² out of 61,484 km², 29.9%), Indonesia (16,150 km² out of 69,470

km², 23.2%), and the Philippines (15,196 km² out of 33,732 km², 45.0%); Table S6). Small island territories have the highest proportion of selected reef areas: Niue (31 km² of 40 km², 77.5%), Vanuatu (1,403 km² of 2,007 km², 69.9%), American Samoa (88 km² of 129 km², 68.2%), Comores (271 km² of 405 km², 66.9%), Christmas Island (16 km² of 25 km², 64.0%), and the Chagos Archipelago (1,816 km² of 2,880 km², 63.1%) each have more than 60% of their national or territorial reef extent selected as priority climate refugia.

The Atlantic–Caribbean shows some of the most substantial gains when refugia criteria are expanded beyond thermal-stress avoidance to include reefs that can resist and recover from bleaching. Our analysis identifies extensive new potential refugia not captured by Beyer et al (2018), including 1,497 km² of resilient reef in Belize (out of 3,293 km² of national reef extent, or 45.5%), 1,480 km² in the Turks and Caicos Islands (out of 5,208 km², 28.4%), 1,101 km² in Panama (out of 2,091 km², or 53%), and 417 km² in Nicaragua (out of 963 km², or 43.3%). These results indicate that the Caribbean may harbour greater resilience potential than previously recognised, offering renewed opportunities to support coral reef futures in a region that nonetheless remains highly vulnerable, characterised by low coral species diversity, intense local human pressures, exposure to severe and repeated marine heatwaves, and recent functional losses including local extinctions of *Acropora* (Manzello et al 2025; see also Chollett et al 2022). These areas reflect refugia signals that emerge when resistance and recovery capacity are evaluated alongside thermal-stress avoidance, using a broader empirical predictor set than the SST- and DHW-based metrics in Beyer et al (2018). Sites such as Belize, Turks and Caicos, and Panama were present in earlier reef extent datasets but did not rank as priorities under thermal-stress avoidance alone. Other notable marine areas that are included in the 50 Reefs plus analysis compared to the Beyer et al (2018) include: New Caledonia (2,011 km² out of 9,547 km², 21.1% of national or territorial reef extent), the Chagos archipelago (1,816 km² of 2,880 km², 63.1%), Vanuatu (1,403 km² of 2,007 km², 69.9%), Micronesia (1,448 km² out of 5,081 km², 28.5%), Palau (640 km² out of 1,880 km², 34.0%), and the Galapagos islands (205 km² out of 692 km², 30.1%).

Our approach builds on Beyer et al (2018), the most comparable global coral reef refugia assessment, by generating explicit predictions of coral cover and community composition validated against observed data, with province-level skill estimates that allow users to calibrate confidence by region (Table S5). Predicting not only where reefs may persist but what kinds of coral communities are likely to survive has direct implications for reef function and recovery potential. Where our identified refugia overlap spatially with Beyer et al's priority bioclimatic units, convergence across independent methodologies strengthens confidence in those locations; where they diverge, differences likely reflect our incorporation of observed coral cover, community composition, and an expanded predictor set (Table S6; see Supporting Information).

Of the 165,922 km² identified as climate-resilient coral reefs, fewer than one-third (46,317 km²; 27.9%) currently fall within protected and conserved areas (UNEP-WCMC and IUCN 2026), leaving 119,605 km² (72.1%) of climate-resilient reefs outside any designated conservation framework. This unprotected majority represents one of the clearest near-term opportunities to

advance Target 3 of the Kunming–Montreal Global Biodiversity Framework, which commits Parties to the Convention on Biological Diversity to conserve 30% of coastal and marine areas by 2030. Targeting expansion toward climate-resilient reefs, rather than reefs selected on opportunity or feasibility alone, would also directly align Target 3 implementation with the long-term persistence of coral reef ecosystems under climate change (Target 8; see also Degemmis et al 2026). Equally important, the 27.9% already inside protected and conserved areas cannot be assumed to be secured: without adequate resourcing, enforcement, and management capacity, these designations risk operating as "paper parks" that deliver neither the ecological outcomes nor the social benefits intended (Gill et al 2017; Stephenson et al 2025). Realising the conservation value of climate-resilient reefs will therefore require both strategic expansion of the protected area network and substantive investment in the effectiveness of what is already designated.

Translating these global figures into action requires spatial information at scales that match how conservation decisions are actually made. Our 250 m gridded predictions offer a substantial improvement in spatial resolution over previous global assessments, such as the 500 km² bioclimatic units of Beyer et al (2018), providing predictive maps of coral condition and community composition at scales relevant to reef management units, MPA network design, and national area-based planning processes. These outputs are intended to complement, rather than replace, local and nationally led conservation planning, supporting Parties seeking to identify candidate sites for Target 3 expansion, prioritise resourcing within existing protected areas, and ground these choices in spatially explicit predictions of where climate-resilient reefs are most likely to persist. Outputs from this study are already being used in specific geographies (e.g., Fiji) to support development of national coral reef action plans.

Limitations and future directions

Several limitations should be considered when interpreting these results. First, the machine-learning models capture statistical rather than mechanistic relationships and thus assume that historical driver–response patterns will continue under future climate conditions. This may underestimate novel future states. Predictor datasets also vary in spatial and temporal resolution, for example, cyclone exposure layers (~200 km) are much coarser than habitat maps (250 m), which can mask fine-scale drivers of resilience. In addition, monitoring data are unevenly distributed across provinces (Fig. S1), and model performance was lowest in regions with sparse field observations (Table S5). These issues underscore the need for more standardized monitoring data, locally calibrated models that incorporate site-specific processes and coral adaptations (McClanahan and Sola 2024), and flexible objective functions that can be adjusted to regional model performance or desired custom weightings by stakeholders. Model structure and parameter choices can also influence outcomes, a pattern documented across coral-reef machine-learning studies (McClanahan 2025).

Second, provincial variation in model performance has direct implications for the refugia prioritization. Where models did not pass accuracy and significance thresholds, no predictions were made rather than contributing uncertain values. For provinces where models passed thresholds but with weaker fits, the per-ecoregion portfolio structure, spatial cohesion

objectives, and 100-run ensemble averaging buffer the prioritization against pointwise prediction error; however, refugia priorities in these provinces should be interpreted as more provisional than those in well-fit provinces (notably Africa-India, Indonesian, Atlantic Caribbean, and Hawaii-Line Islands). Improved field monitoring in data-sparse provinces remains the most direct path to reducing this uncertainty in future assessments. While our approach represents a methodological advance over threat-ranking frameworks (e.g., Beyer et al 2018) by generating ecologically grounded predictions of coral cover and composition, we caution that global predictions require further ground-truthing and validation by conservation practitioners to be a sufficient basis for investment decisions globally. Given the scale of investment increasingly directed toward coral reef conservation, site selection should draw on multiple lines of evidence rather than any single model output. Our predictions are intended as one such resource, with SHAP values (Fig. 2) and z-score distributions across prioritisation objectives (Fig. S5) providing transparent information about why particular reefs are identified as climate-resilient, complementing local ecological knowledge, site-level assessments, and adaptive management in guiding future conservation investments.

Third, the prioritization does not incorporate governance feasibility, management capacity, or implementation costs, factors that ultimately determine whether climate-resilient reefs can be effectively conserved and managed. For example, many protected and conserved areas remain under-resourced (Gill et al 2017; Stephenson et al 2025), and assessing conditions of socioeconomic and political enabling conditions, compliance and enforcement, and long-term sustainable financing for conservation will be key to enduring ecological outcomes in these critical areas of climate resilience.

Looking forward, several refinements would strengthen future refugia assessments and improve model performance: integrating moderate- to high-resolution environmental predictors (e.g., water quality, hydrodynamics), using hierarchical and transfer-learning approaches to leverage local datasets, more monitoring information available for coral genera and life history abundance, and updating prioritizations iteratively as climate conditions and monitoring information evolve. Despite these constraints, the framework provides an improved and scalable global framework for identifying climate resilient reefs. Coupled with local knowledge, adaptive management, and national policies, these results can help guide durable conservation actions that support coral-reef ecosystem services into the mid-century.

Conclusions

This study shows that combining empirical coral reef observations with machine-learning predictions and multi-objective spatial optimization expands the identification of candidate climate refugia at global scale. By integrating present and projected persistence of coral cover and community composition, we provide the first high-resolution assessment of where reefs are most likely to endure severe mid-century warming. Despite widespread and increasing thermal stress, we find large and spatially distinct areas with ecological and environmental conditions that support coral reef persistence. These priority areas are concentrated in a subset of countries but occur across most reef regions, highlighting opportunities to strategically align conservation and management actions to the places offering the greatest long-term ecological

and societal returns. These results argue against framing coral reef futures around a binary global tipping point. Climate-driven coral decline is real, but spatially heterogeneous, and every fraction of a degree of avoided warming preserves options for coral reef futures.

Acknowledgements. The research was funded by a grant from the Bloomberg Ocean Initiative to the Wildlife Conservation Society. We thank Kim Fisher and Iain Caldwell for their work incorporating coral life history percent cover into MERMAID aggregate summaries. We are also grateful to colleagues and subject-matter experts who provided valuable input during early rounds of model development and review, helping refine the analytical framework and interpretation of results. We thank two anonymous reviewers for constructive comments that improved the analyses and manuscript.

Data Availability. All code used in modelling and spatial prioritization is available at https://github.com/Kylezx1/zawada_et_al_2026_global_coral_climate_refugia. Publicly available datasets used in modelling are available on request to the authors.

References

Allen Coral Atlas 2022 Imagery, maps and monitoring of the world's tropical coral reefs Zenodo (doi: 10.5281/zenodo.3833242)

Andréfouët S, Maële B, Stéphane G and Antoine G 2024 Evaluation of the Allen Coral Atlas benthic habitat map product for New Caledonia using representative habitat observations from a multi-species fishery assessment *Coral Reefs* **43** 523–540

Beck M W, Heck N, Narayan S, Menéndez P, Reguero B G, Bitterwolf S, Torres-Ortega S, Lange G-M, Pfliegner K, Pietsch McNulty V and Losada I J 2022 Return on investment for mangrove and reef flood protection *Ecosyst. Serv.* **56** 101440

Beyer H L et al. 2018 Risk-sensitive planning for conserving coral reefs under rapid climate change *Conserv. Lett.* **11** e12587 (doi: 10.1111/conl.12587)

Bloomberg Philanthropies 2021 50 Reefs Landscape Assessment: Progress, Lessons Learned, and Future Opportunities (Bloomberg Philanthropies Vibrant Oceans Initiative)

Burke L, Reyttar K, Spalding M and Perry A 2011 *Reefs at Risk Revisited: Technical Notes on Modeling Threats to the World's Coral Reefs* (Washington, DC: World Resources Institute)

CBD 2022 Kunming–Montreal Global Biodiversity Framework... Secretariat of the Convention on Biological Diversity, Montreal, Canada

Chen T and Guestrin C 2016 XGBoost: a scalable tree boosting system *Proc. 22nd ACM SIGKDD Int. Conf. Knowledge Discovery and Data Mining* (New York: ACM) pp 785–794 (doi: 10.1145/2939672.2939785)

Chollett I, Escovar-Fadul X, Schill S R, Croquer A, Dixon A M, Begger M, Shaver E, Pietsch McNulty V and Wolff N H 2022 Planning for resilience: incorporating scenario and model

uncertainty and trade-offs when prioritizing management of climate refugia *Glob. Change Biol.* **28** 4054–4068

Cinner J E, Maire E, Huchery C, MacNeil M A, Graham N A J, Mora C, McClanahan T R, Barnes M L, Kittinger J N, Hicks C C, D'Agata S et al 2018 Gravity of human impacts mediates coral reef conservation gains *Proc. Natl Acad. Sci. USA* **115** E6116–E6125

Cornwall C E, Comeau S, Kornder N A, Perry C T, van Hooidonk R, DeCarlo T M, Pratchett M S, Anderson K D, Browne N and Carpenter R 2021 Global declines in coral reef calcium carbonate production under ocean acidification and warming *Proc. Natl Acad. Sci. USA* **118** e2015265118

Darling E S, Alvarez-Filip L, Oliver T A, McClanahan T R and Côté I M 2012 Evaluating life-history strategies of reef corals from species traits *Ecol. Lett.* **15** 1378–1386

Darling E S, McClanahan T R and Côté I M 2013 Life histories predict coral community disassembly under multiple stressors *Glob. Change Biol.* **19** 1930–1940

Darling E S et al. 2019 Social–environmental drivers inform strategic management of coral reefs in the Anthropocene *Nat. Ecol. Evol.* **3** 1341–1350

DeCarlo T M and Whitaker H V 2025 Coral bleaching projections for the Great Barrier Reef throughout the 21st century *Geophys. Res. Lett.* **52** e2025GL119834

DeGemmis A et al. 2026 Coral reef commitments are largely absent from national biodiversity and climate frameworks *Mar. Policy* in review

Eyring V, Bony S, Meehl G A, Senior C A, Stevens B, Stouffer R J and Taylor K E 2016 Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization *Geosci. Model Dev.* **9** 1937–1958 (doi: 10.5194/gmd-9-1937-2016)

Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner S D and Hoegh-Guldberg O 2013 Limiting global warming to 2 °C is unlikely to save most coral reefs *Nat. Clim. Change* **3** 165–170

Gill D A et al. 2017 Capacity shortfalls hinder the performance of marine protected areas globally *Nature* **543** 665–669

Gonzalez-Espinosa P C and Donner S D 2021 Cloudiness reduces the bleaching response of coral reefs exposed to heat stress *Glob. Change Biol.* **27** 3474–3486

Gurobi Optimization LLC 2026 Gurobi Optimizer Reference Manual (<https://www.gurobi.com>)

Hausfather Z 2025 An assessment of current policy scenarios over the 21st century and the reduced plausibility of high-emissions pathways *Dialogues Clim. Change* **2** 26–32

- Hoegh-Guldberg O, Skirving W, Dove S G, Spady B L, Norrie A, Geiger E F, Liu G, De La Cour J L and Manzello D P 2023 Coral reefs in peril in a record-breaking year *Science* **382** 1238–1240
- Hoegh-Guldberg O, Kennedy E V, Beyer H L, McClennen C and Possingham H P 2018 Securing a long-term future for coral reefs *Trends Ecol. Evol.* **33** 936–944
- Hughes T P, Kerry J T, Álvarez-Noriega M et al 2017 Global warming and recurrent mass bleaching of corals *Nature* **543** 373–377
- Kalmus P, Ekanayaka A, Kang E, Baird M and Gierach M 2022 Past the precipice? Projected coral habitability under global heating *Earth's Future* **10** e2021EF002608
- Keith S A, Baird A H, Hughes T P, Madin J S and Connolly S R 2013 Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution *Proc. R. Soc. B* **280** 20130818
- Keppel G, Van Niel K P, Wardell-Johnson G W, Yates C J, Byrne M, Mucina L, Schut A G T, Hopper S D and Franklin S E 2012 Refugia: identifying and understanding safe havens for biodiversity under climate change *Glob. Ecol. Biogeogr.* **21** 393–404
- Klein S G, Roch C and Duarte C M 2024 Systematic review of the uncertainty of coral reef futures under climate change *Nat. Commun.* **15** 2224
- Kleypas J A, McManus J W and Meñez L A 1999 Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* **39** 146–159
- Li X and Donner S D 2022 Lengthening of warm periods increased the intensity of warm-season marine heatwaves over the past 4 decades *Clim. Dyn.* **59** 2643–2654
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H and van Woesik R 2001 Coral bleaching: the winners and the losers *Ecol. Lett.* **4** 122–131
- Lundberg S M, Erion G G and Lee S-I 2019 Consistent individualized feature attribution for tree ensembles *arXiv* 1802.03888
- Lyons M B et al. 2024 New global area estimates for coral reefs from high-resolution mapping *Cell Rep. Sustain.* **1** 100015
- MacNeil M A, Mellin C, Matthews S, Wolff N H, McClanahan T R, Devlin M, Drovandi C, Mengersen K and Graham N A J 2019 Water quality mediates resilience on the Great Barrier Reef *Nat. Ecol. Evol.* **3** 620–627 (doi: 10.1038/s41559-019-0832-3)
- Manzello D P et al. 2025 Heat-driven functional extinction of Caribbean Acropora corals from Florida's Coral Reef *Science* **390** 361–6
- Markowitz H 1952 Portfolio selection *J. Finance* **7** 77–91

- McClanahan T R 2023 Local heterogeneity of coral reef diversity and environmental stress provides opportunities for small-scale conservation *Divers. Distrib.* **29** 1324–1340
- McClanahan T R 2025 Evaluating coral reef hazards requires both explanatory and predictive models *Coral Reefs* **44** 2235–2247
- McClanahan T R and Azali M K 2021 Environmental variability and threshold model's predictions for coral reefs *Front. Mar. Sci.* **8** 778121
- McClanahan T R and Sola E 2024 Comparing modeled predictions of coral reef diversity along a latitudinal gradient in Mozambique *Front. Ecol. Evol.* **12** 1450383
- McClanahan T R et al. 2019 Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño *Nat. Clim. Change* **9** 845–851
- McClanahan T et al. 2020 Highly variable taxa-specific coral bleaching responses to thermal stresses *Mar. Ecol. Prog. Ser.* **648** 135–151
- McClanahan T R, Azali M K, Muthiga N A, Porter S N, Schleyer M H and Guillaume M M 2024a Complex multivariate model predictions for coral diversity with climatic change *Ecosphere* **15** e70057
- McClanahan T R, Darling E S, Beger M, Fox H E, Grantham H S, Jupiter S D, Logan C A, Mcleod E, McManus L C, Oddenyo R M and Surya G S 2024b Diversification of refugia types needed to secure the future of coral reefs subject to climate change *Conserv. Biol.* **38** e14108
- Mellin C, Brown S, Heron S F and Fordham D A 2025 CoralBleachRisk—global projections of coral bleaching risk in the 21st century *Glob. Ecol. Biogeogr.* **34** e13955
- Morais J, Almeida P M, Avelino C D, Souza M C A, Cardoso A P L R, Gurgel A L A R, Soares M O and Santos B A 2026 Risk or relief? The influence of river plumes on coral bleaching and disease *Mar. Pollut. Bull.* **222** 118741
- Nakamura T, Van Woesik R and Yamasaki H 2005 Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral *Acropora digitifera* *Mar. Ecol. Prog. Ser.* **301** 109–118
- Perry C T, Murphy G N, Kench P S, Smithers S G, Edinger E N, Steneck R S and Mumby P J 2013 Caribbean-wide decline in carbonate production threatens coral reef growth *Nat. Commun.* **4** 1402
- Pratchett M S, Hoey A S, Wilson S K, Messmer V and Graham N A J 2011 Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss *Diversity* **3** 424–452
- Raschka S 2018 Model evaluation, model selection, and algorithm selection in machine learning *arXiv* 1811.12808

ReefBase 1996 ReefBase: a global database of coral reefs and their resources ICLARM, Manila, Philippines

Schmidt G M, Wall M, Taylor M, Jantzen C and Richter C 2016 Large-amplitude internal waves sustain coral health during thermal stress *Coral Reefs* **35** 869–881

Spady B L et al. 2026 The 4th global coral bleaching event: ushering in an era of near-annual bleaching *Coral Reefs* in press

Spalding M D et al. 2007 Marine ecoregions of the world: a bioregionalization of coastal and shelf areas *Bioscience* **57** 573–583

Stephenson F et al. 2025 Quality of marine protected areas is critical to achieving global biodiversity targets *npj Ocean Sustain.* **4** 63

Sully S and van Woelk R 2020 Turbid reefs moderate coral bleaching under climate-related temperature stress *Glob. Change Biol.* **26** 1367–1373

UNEP-WCMC, WorldFish Centre, WRI and TNC 2021 Global distribution of coral reefs Version 4.1 UNEP-WCMC, Cambridge, UK (doi:10.34892/t2wk-5t34)

UNEP-WCMC and IUCN 2026 Protected Planet: The World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM). Available at: www.protectedplanet.net.

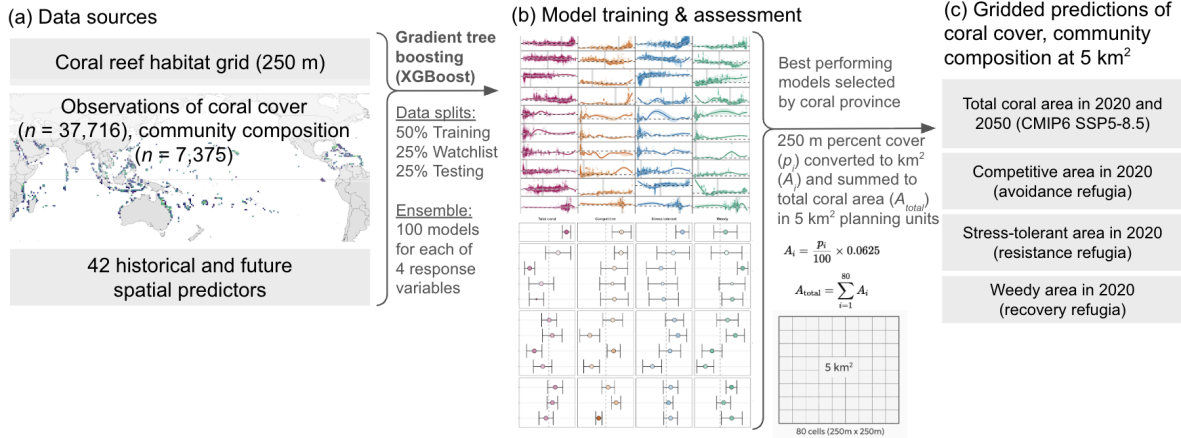
Van Vuuren D P et al. 2026 The Scenario Model Intercomparison Project for CMIP7 (ScenarioMIP-CMIP7) *Geosci. Model Dev.* **19** 2627–56

Zawada K, Darling E S, Jupiter S, McClanahan T and Maina J 2026 Global 250 m coral reef prioritization layer v1.0 Zenodo (doi: 10.5281/zenodo.18686274)

Zeng K, He S and Zhan P 2025 Inevitable global coral reef decline under climate change-induced thermal stresses *Commun. Earth Environ.* **6** 827

Zinke J et al. 2018 Gradients of disturbance and environmental conditions shape coral community structure *Divers. Distrib.* **24** 605–620

Machine-learning predictions



Spatial prioritization of climate refugia

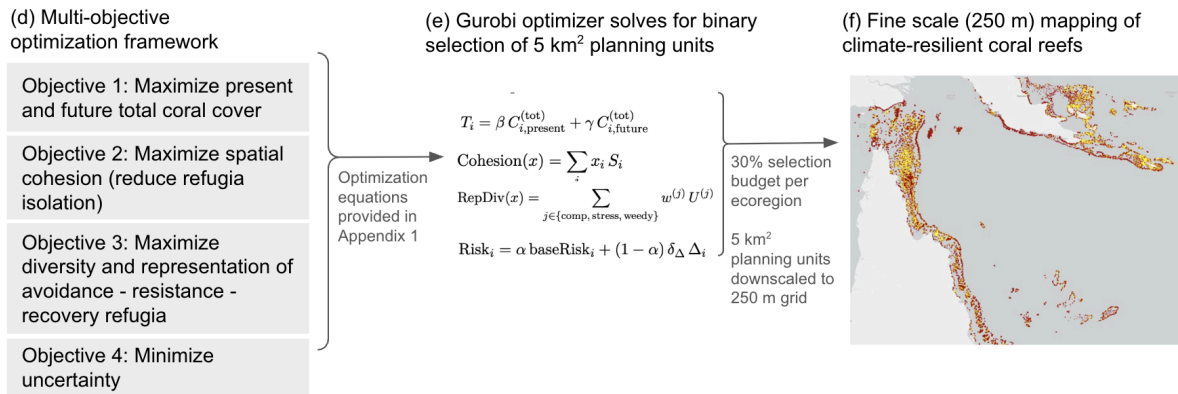


Figure 1. Overview of the analytical workflow used to model global coral cover and coral community composition and to prioritize climate-resilient reef refugia. (a) Coral cover and community observations were linked to a 250 m global coral reef habitat grid and 42 historical and future environmental predictors. (b) We trained ensembles of XGBoost gradient-boosted tree models for each response variable, evaluated model performance by coral province, and predicted percent cover of four coral responses at 250 m resolution. (c) Spatial predictions were converted to coral area (km^2) of total coral cover and three life-history types (competitive, stress-tolerant, and weedy) on a 5 km^2 grid of planning units. (d) A multi-objective optimization framework was used to identify portfolios of climate refugia that maximize present and future coral area, spatial cohesion, and life-history representation while minimizing uncertainty. Optimization was solved as a binary integer program in Gurobi under a 30 percent per-ecoregion budget. (e) Selected 5 km^2 planning units were downscaled to 250 m to map fine-scale distributions of climate-resilient coral reefs (see Supporting Information).

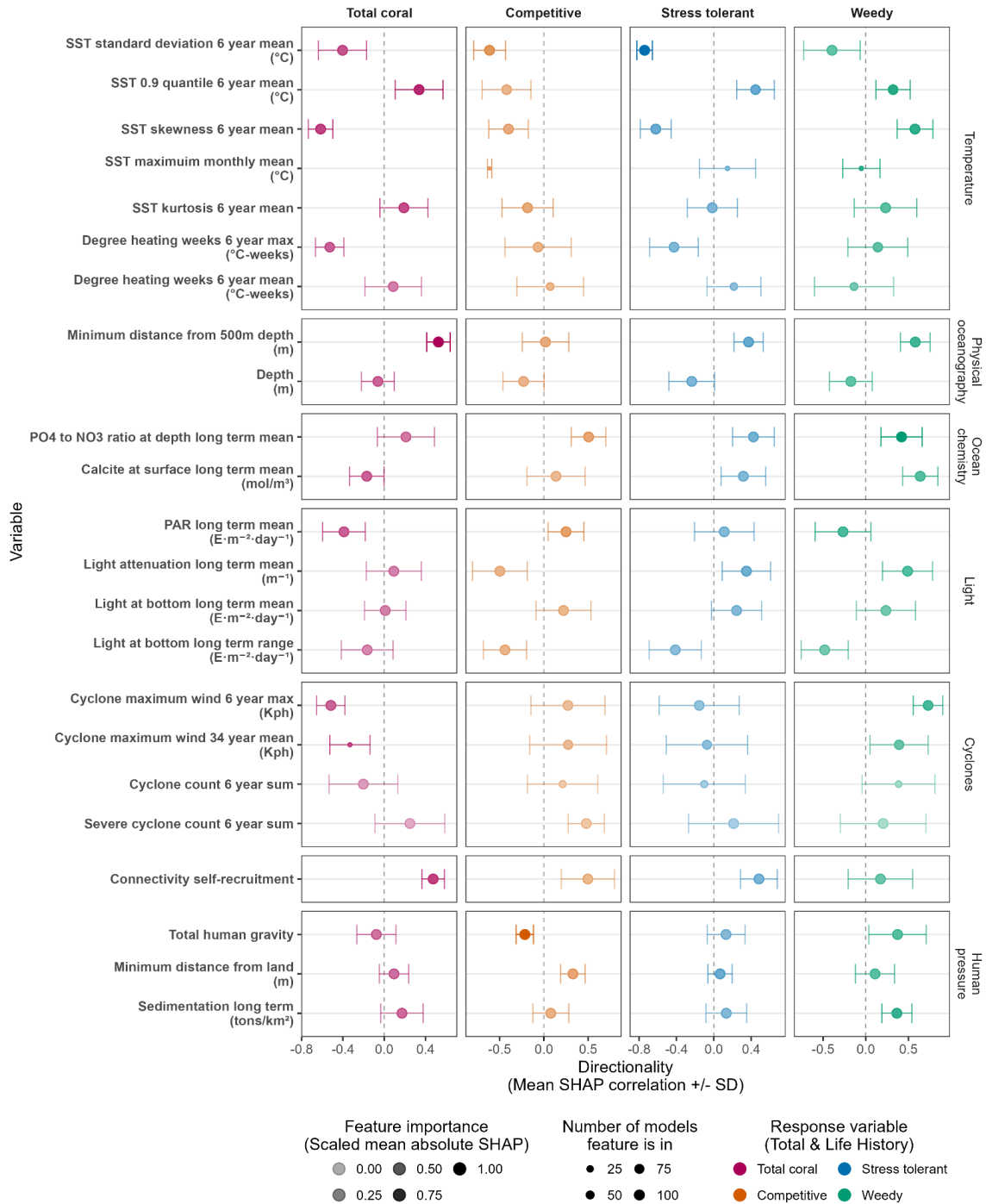


Figure 2. Direction and relative importance of environmental drivers of cover differ among total coral cover and life-history groups. Results are based on 100-model machine-learning ensembles for each response. Correlations represent Pearson coefficients between each predictor and its SHAP contribution to predicted cover. Points show mean correlations across models, with point size indicating the frequency with which each variable was retained after variance-inflation screening. Colour saturation corresponds to feature importance (mean absolute SHAP value). Error bars denote standard deviations, and vertical dashed lines indicate zero correlation. Corresponding response curves and partial dependence plots are provided in Figure S3.

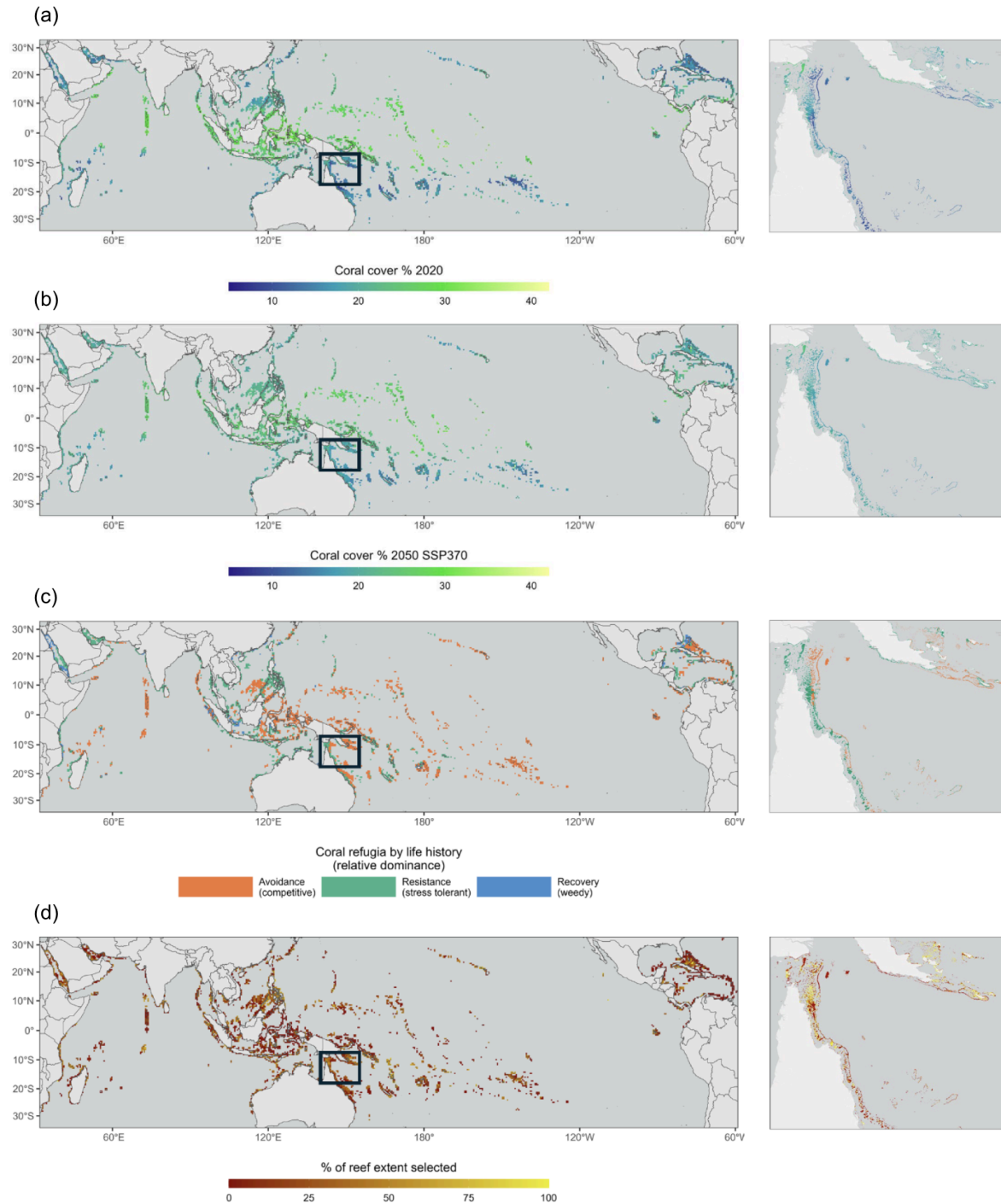


Figure 3. Machine learning and spatial optimization identify contemporary coral refugia from predicted coral cover and life-history composition. (a) Predicted 2020 coral cover from 100-model ensembles. (b) Predicted 2050 cover under CMIP6 SSP3-7.0 (see Figure S6 for SSP5-8.5 predictions). (c) Avoidance, resistance, and recovery refugia based on dominant life-history groups. (d) Global prioritization of climate-resilient reefs using a 30% per-ecoregion portfolio that favours high cover, diverse life histories, spatial cohesion, and low ecological risk. Left panels show global patterns at 50 km resolution for visualization of global patterns; right panels illustrate high-resolution examples in the northern Great Barrier Reef and southern Papua New Guinea.

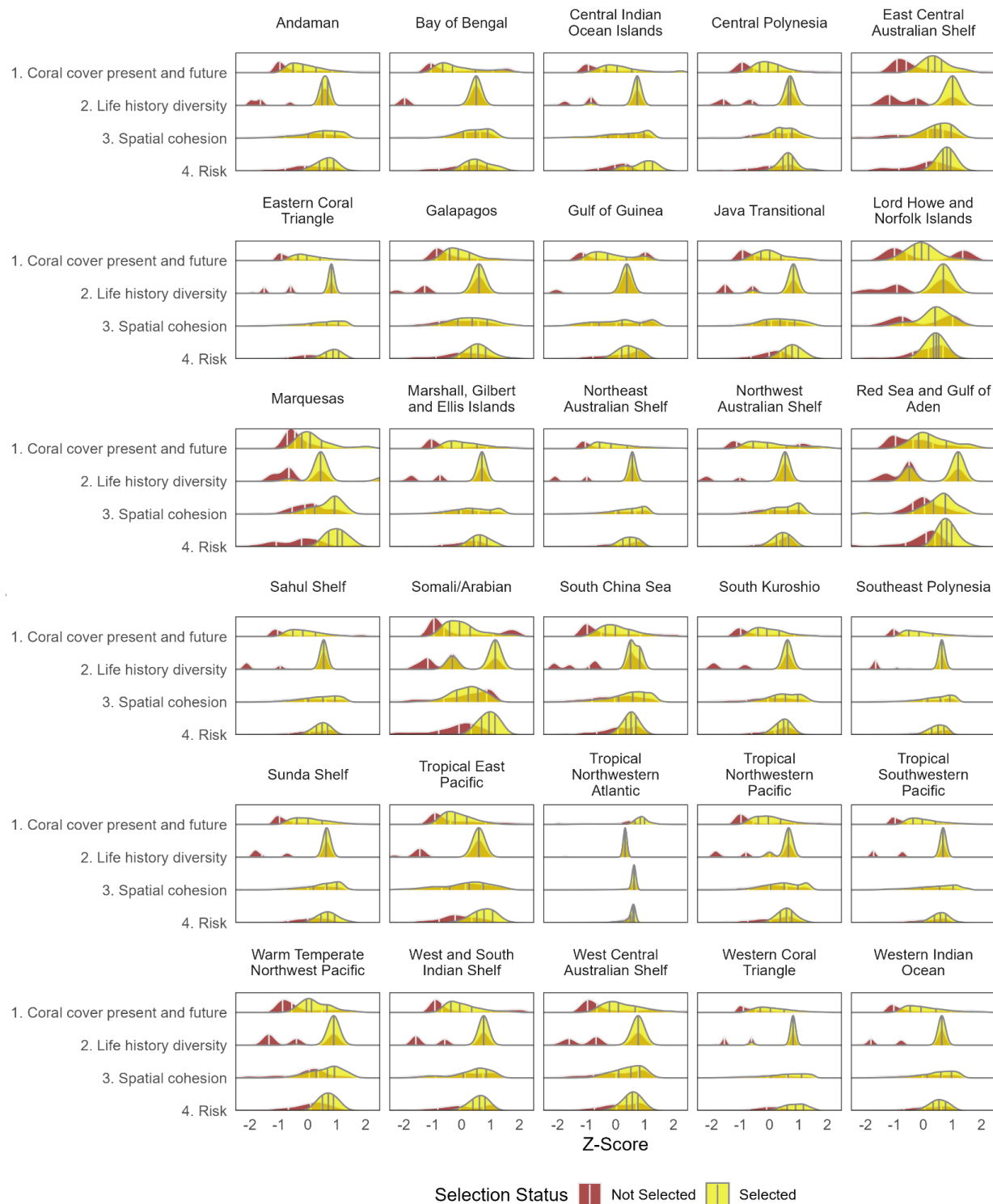


Figure 4. Density plots showing the relative influence of each objective function on prioritization outcomes across marine ecoregions. Distributions represent normalized Z-scores for all planning units within each ecoregion. Grey curves indicate units not selected in the optimization, and red curves indicate units selected in the final 30% portfolios. Overlapping densities illustrate how objective contributions differed between selected and unselected areas and how these patterns varied among ecoregions.

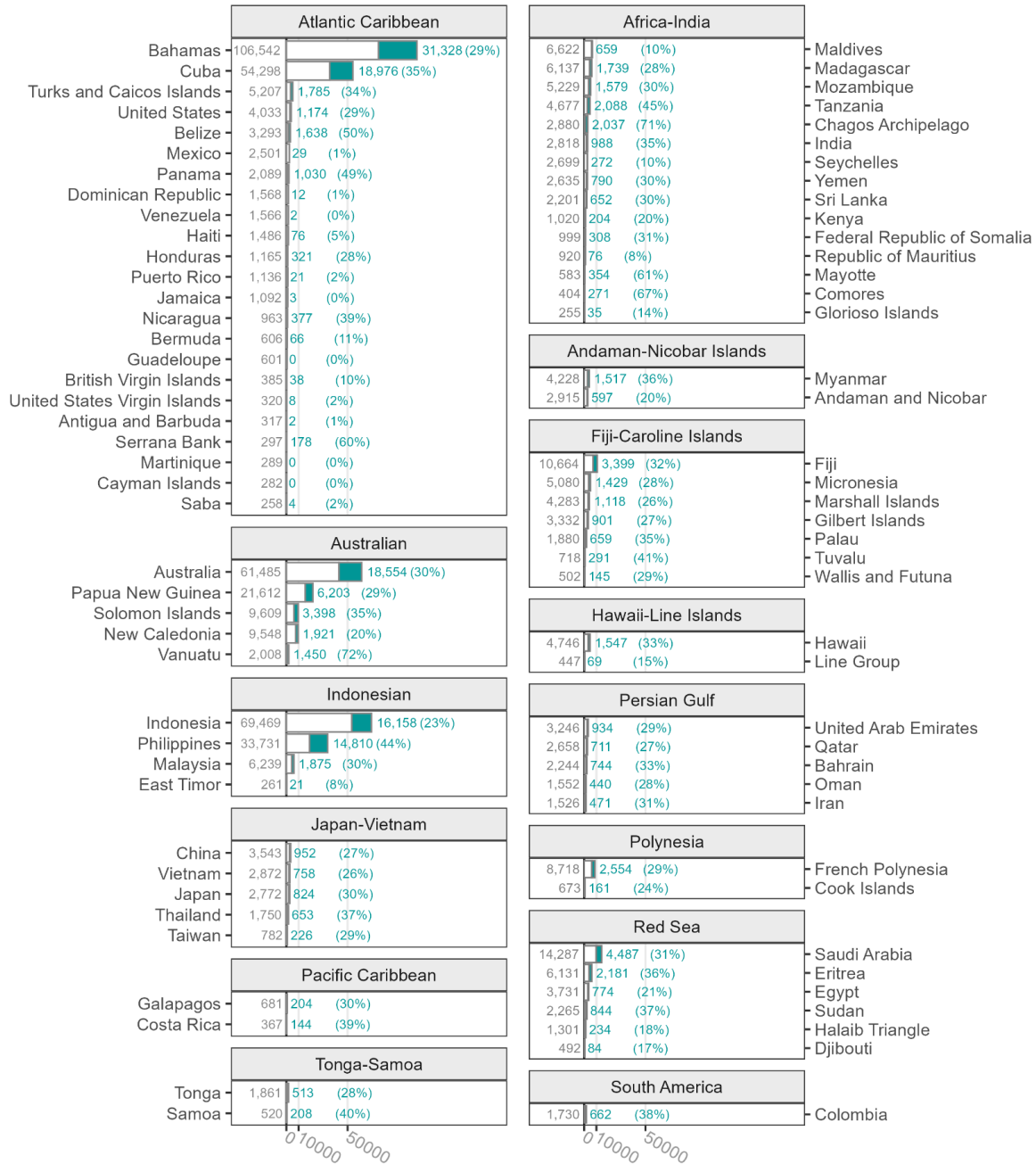


Figure 5. Climate refugia for coral reefs are unevenly distributed across coral reef countries and territories. Exclusive Economic Zones (EEZs) define national, territorial, and jurisdictional units, grouped by coral province. Bars show coral reef habitat that was selected (blue) or not selected (white), with grey labels indicating total reef extent (km²). Blue labels show the area of climate resilient reefs and percent of total reef extent. Countries and territories with more than 250 km² of reef area are shown; full results are provided in Table S6.