EXECUTIVE SUMMARY

Forecasting Climate Sanctuaries for Securing the Future of Coral Reefs

Vibrant Oceans Initiative Whitepaper | APRIL 2022

Since the launch of the 50 Reefs portfolio in 2018, the world's coral reefs have experienced continued climate change impacts that have led to mass coral bleaching and mortality. Drawing on thirty years of research, we highlight the environmental and biological factors that predict the ongoing climate impacts of coral reefs, and explore the potential for adaptation, acclimation and stress tolerance of coral reefs. We propose to expand the 50 Reefs approach into three types of climate change sanctuaries: avoidance, resistance, and recovery refugia. While previous efforts have typically focused on avoidance sanctuaries, defined as coral reef locations that have until now avoided climate-change related stresses and are predicted to experience less future acceleration of stresses (e.g., the 50 Reefs), there is a renewed urgency to safeguard locations that can also display resistance to climate exposure or show rapid recovery after bleaching events.

The 50 Reefs portfolio remains a good investment for avoidance sanctuaries but becomes more robust when resistance and recovery sanctuaries are included. We recommend that future portfolios should include reefs with broader environmental, ecological, and genetic characteristics that specifically underscore resistance and recovery. However, testing the predictions of these models remains crucial in order to evaluate the expectation that reefs within proposed sanctuaries are healthier (i.e., coral cover and reef fish biomass above key thresholds, higher diversity) than reefs outside of proposed sanctuaries. Ultimately, a holistic approach integrating sanctuaries and ecosystem services can inform how investments in coral reef conservation can safeguard key reef functions of maintained carbonate production of reef corals, coral adaptation/acclimation processes, and reef fisheries production. As impacts of climate change accelerate and result in ecological surprises or adaptation/acclimation mechanisms, future modeling efforts should go beyond excess heat and temperatures to integrate globally comparable datasets of ecological surveys, hydrodynamic modeling, genetics, and remotely sensed environmental data layers.

We conclude with specific recommendations for governments, funders, conservation organizations, and stakeholders on how to promote the persistence and survival of tropical coral reefs in order to minimize the loss of reef services to humanity under the increasing stress of climate change. These recommendations include:

- **Continue with the 50 Reefs approach (i.e., climate change avoidance sanctuaries) as a priority for investment in coral reef conservation.**
- **Expand the 50 Reefs conservation portfolio for climate change to include coral resistance and recovery sanctuaries.**
- **Increase support for regional evaluations of the health of the 50 Reefs portfolio, and sustainable financing initiatives to support the implementation of regional portfolios.**
- **Catalyze large-scale, data-driven coral reef monitoring efforts to test and develop new models and predictions of climate sanctuaries.**
- **Use the latest climate coral reef science to guide investments, especially as the impacts of climate change accelerate and produce novel environmental stresses and responses among reefs.**
- **Embrace a holistic approach to the management of 50 Reefs sites, including connections to broader seascapes, fisheries and water quality management, mitigation of other pressures (e.g., industrial development), so that effective and equitable management has measurable benefits for coral reefs and coastal communities.**

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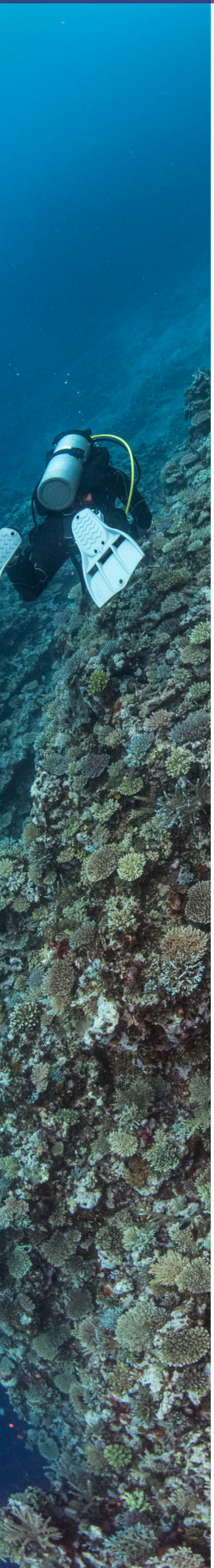
FORECASTING CLIMATE SANCTUARIES FOR SECURING THE FUTURE OF CORAL REEFS



Authors: Tim McClanahan[1], Emily Darling[1], Remy Oddenyo[2], Gautam Surya[3], Maria Beger[4], Helen Fox[5], Stacy Jupiter[6], Lizzie McLeod[7], Lisa McManus[8], Robert van Woesik[9], Hedley Grantham[3], Cheryl Logan[10], Joseph Maina[11], Vardhan Patankar[12], Amelia Wenger[1,13], Jens Zinke[14]

Background

Not all coral reef environments and associated species are the same. This is especially true when viewed over the complex ecological, evolutionary and geological history of the Earth. This history has created a diversity of species, their variable and complex ecological communities, and emergent reef communities. It is also the basis for the varied responses coral reefs have to environmental change. While the changes occurring now are rapid, extensive, and intensive, there are some historical precedents that have promoted adaptation to changing conditions. For example, reef environments show predictable changes to stress across reef zones, along inshore to offshore gradients, from windward to leeward sides of islands, across archipelagos, across seasons, and along longitudinal and latitudinal gradients (McClanahan et al. 2007, 2011, 2019, 2020a,b; Selmoni et al. 2021). Therefore, there is no one type of response that coral reefs have to adjust to climate change, but rather there are potentially a suite of responses associated with avoidance, resistance, and recovery to climate impacts. This diversity of responses and the potential for conservation interventions to access and enhance these diverse responses provide hope for adaptation and persistence of reefs that are experiencing unprecedented rapid change.

Ecosystems are vulnerable to collapse when stressed beyond their capacity to adapt. For coral reefs, this collapse is typically associated with the loss of sensitive species or large colonies, declines in live coral cover, or transitions to macroalgae, sponge, corallimorph, or soft coral regimes (i.e., non-calcifiers) (McClanahan et al. 2002; Reimer et al. 2021). Yet, such outcomes are dependent on the complex interaction among the elements of exposure and sensitivity, and on the adaptive capacity of the assemblages (Cinner et al. 2013). Climate change increases extreme thermal exposure, increased acidity, and declining oxygen but the effects depend on the context of natural variability (McClanahan and Maina 2003; Sully et al. 2020; Donovan et al. 2021; Dixon et al. 2022). For example, natural patterns of wave exposure, currents, rainfall, tides, seasons, and inter-annual oceanographic oscillations contribute to the frequency, intensity, and duration of exposure to climate change pressures. In addition, patterns of exposure to human-influenced pressures like overfishing or pollution are superimposed on these natural rhythms. Both types of exposures can be considered as chronic and acute stressors, and in most cases human influences are aggravating the chronic stressors and accentuating acute exposure (He and Silliman 2020). These interactions have consequences for species and communities based on their traits and given that some species will be more adapted to different types of disturbances (Figure Annex 1). Such biological reorganization has consequences for ecosystem services, such as shoreline protection and fisheries production, two critical goods and ecosystem services of coral reefs (McClanahan et al. 2002).

Following the first global bleaching events, coral reef science has investigated responses to climate disturbances and developed approaches to defining and identifying potential refuges or sanctuaries for coral reefs to climate change. Notably, sanctuaries are priority locations to manage non-climate pressures (e.g., overfishing, pollution, disease, dredging, etc.) that could degrade corals within climate sanctuaries. Ultimately, coral reefs have the best chance to survive and function within climate refuges where other local pressures are well managed or mitigated. Here, we focus on scientific efforts to

1 Wildlife Conservation Society, Marine
2 Wildlife Conservation Society, Kenya
3 Wildlife Conservation Society, Forests and Climate Change
4 University of Leeds
5 Coral Reef Alliance
6 Wildlife Conservation Society, Melanesia
7 The Nature Conservancy
8 University of Hawai'i
9 Florida Institute of Technology
10 California State University Monterey Bay
11 Macquarie University
12 Wildlife Conservation Society, India
13 University of Queensland
14 University of Leicester

identify resilient corals and refuges to climate change, recognizing complementary efforts to assess policy (Degemmis et al. 2021), governance (Andrachuk et al. 2022a), sustainable finance (Victurine et al. 2022), water quality management (Wakwalla et al. 2022), and small-scale fisheries (Andrachuk et al. 2022b).

Coral responses to climate disturbances

Acute and chronic disturbances can provide a useful framework to describe the impacts of climate change on coral reefs. Acute stressors are defined as episodic stresses that may periodically exceed thresholds of optimal or livable conditions for the organisms. For coral reefs, acute thermal stresses are mostly evaluated as short-term deviations from the above warm-season chronic stress. Excess heat is the most frequently evaluated stress on coral reefs and is most frequently measured relative to a mean summer baseline (i.e., 3 hottest months) for the period for which there is time-series data obtained from satellite measurements. These evaluations are also known as "HotSpots", which are quantified as the accumulation of thermal stress over time, or as degrees of heating over a specified period, often the three warmest months, or 12 warmest weeks of summer (e.g., degree heating weeks, DHWs). Acute stresses, therefore, largely lie outside of the envelope of normal environmental conditions (i.e., 95% confidence intervals) and usually reoccur among rather than within years. Typically, acute disturbance provokes the dysfunction of the coral animal and microscopic algae living in the animal host. Such dysfunctionality leads to the loss of color, or "bleaching", and the loss of production and coral health. Bleaching can be an adaptation to reduce mortality of corals but is often a final "bailing response" prior to mortality. Coral bleaching can lead to differential mortality and leads to the reorganization of the community away from vulnerable taxa and towards resilient taxa (Loya et al. 2001; McClanahan et al. 2020a). This change can be both persistent and temporary, depending on recovery potential. Much of this response may depend on historical exposure and the intensity and frequency of the past and current disturbances.

Chronic stressors, on the other hand, are defined as frequently recurring deviations from baseline conditions, which can either stimulate tolerant or adverse responses of affected organisms. Chronic stressors include important short-term elements of stress, such as the daily to seasonal changes in tides, light, and temperatures. Chronic stressors are also part of the longer-term environmental history of reefs at both ecological and evolutionary scales. Thus, this environmental and regional context of chronic stress is increasingly being understood as critical for evaluating acute responses to climate change, which are often typified by large-scale coral bleaching and mortality. However, some acute disturbances can interact with chronic stressors, for example inter-annual events are part of regular ocean oscillations, such as the El Niño Southern Oscillation and the Indian Ocean Dipole oscillations, which have been recurrent over the Earth's history. Thus, the differences between acute and chronic stress can depend on adaptive capacity, or some form of "memory", induced by past exposure, across various time scales. Functional traits and genetics, and the frequency of historical exposures, therefore, may influence adaptation (Box 1). Ultimately, high levels of acute and chronic disturbance will shift coral communities towards smaller (McClanahan et al. 2008) or less diverse (Lachs et al. 2021) colonies that can precipitate a regime shift to macroalgae or soft substrate dominance (e.g., 'rebound' or 'regime' shifts; Graham et al. 2015).

While chronic and acute stresses are simplifying concepts that help to classify the complexity of environmental change, these concepts provide a useful framework for making predictions for each of the three proposed sanctuary types: avoidance, resistance, and recovery sanctuaries. For example, acute and chronic stressors can classify reefs by the environmental conditions that influence them, which in turn can affect the composition of coral communities and ecosystem service proxies, such as coral cover and fish stocks (Figure A1). Any specific reef may reflect some mosaic of coral taxa or functional traits (e.g., life histories, Darling et al. 2012) dependent on the local history of environmental exposure. A healthy reef is expected to have a diversity of coral taxa and traits needed for the community to adapt to changing environments. In some cases, the environment may be simply too extreme for any of these reefs to be colonized by anything other than non-coral taxa that have lower sensitivity to exposure. This end state occurs as the environment changes towards conditions outside the coral niche (i.e., warm, stable, high light, and low nutrient conditions), leading to the loss of living hard coral and reef assemblages that are unable to supply the services of shoreline protection and fisheries production.

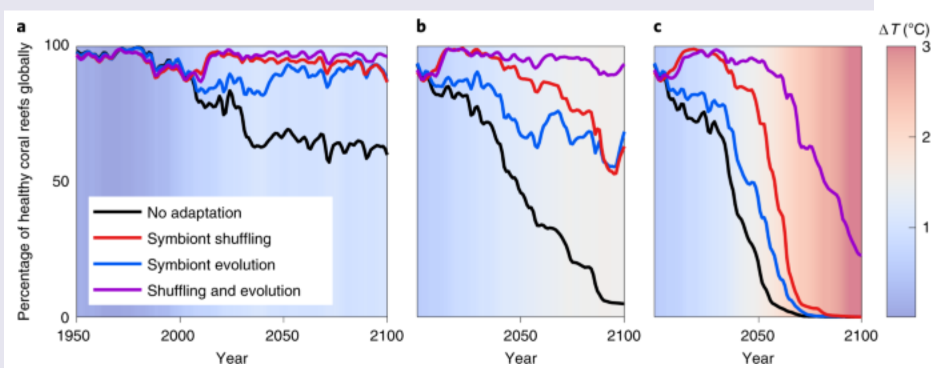
Box 1 | **MODELING ADAPTATION POTENTIAL**

Evolutionary change can occur on ecological timescales (Hendry 2017). As such, researchers are increasingly applying mechanistic eco-evolutionary models to assess the potential of corals to adapt under a changing environment. These models typically simulate cover through time of single or multiple coral populations, along with changes to thermal optima or the presence of warm-adapted alleles based on current understanding of physiological, genetic, and demographic processes that can impact coral persistence (Bay et al. 2017; Logan et al., 2021; Matz et al., 2018; Matz et al., 2020; McManus et al., 2021; Walsworth et al., 2019). Putative ecological and evolutionary responses are typically included in such models, such as the increasing probability of coral bleaching and mortality under rising temperatures (Logan et al. 2014), and the evolution of the optimal growth temperature under directional selection. Some models also incorporate interspecific competition, usually between coral and macroalgae or among multiple coral species (McManus et al. 2021; Logan et al. 2021; Walsworth et al., 2019). The inclusion of these responses allows researchers to explicitly test the impacts of projected climate stressors on coral populations and communities based on lab- and field-derived relationships. Furthermore, these models can be implemented at local, regional, or global scales, and can respond to ocean circulation patterns and climate projection outputs (e.g., temperature and pH) under multiple emissions scenarios.

Coral eco-evolutionary models can be used to identify reef locations and reef characteristics that are particularly vulnerable or resilient to future stressors (Walsworth et al. 2019). Additionally, they can test the relative importance of different adaptation mechanisms, such as coral host evolution, symbiont evolution, or changes in symbiont community composition (Logan et al., 2014, Logan et al., 2021). Another strength of this approach is that demographic and genetic connections among coral populations driven by dispersal can also be incorporated, allowing for the inclusion of both local- and regional-scale processes (Matz et al., 2018; Matz et al., 2020; McManus et al. 2020). Such models are thus uniquely suited to address questions regarding the efficacy of (1) different management interventions such as increasing local protection, outplanting, or assisted migration, and (2) the efficacy of alternative spatial management strategies, to determine where we should allocate effort.

A recent National Academy of Sciences report emphasized the need for such models to inform managers on the potential benefits and risks of long-term human interventions (NRC, 2019). For example, a recent study by Condie et al. (2021) used a coral reef meta-community model of the Great Barrier Reef to examine if and how multiple interventions would increase coral persistence under future warming scenarios, including introduction of heat tolerant corals and regional shading. They found that the most effective management strategies included multiple interventions deployed at large scale compared with any single intervention alone. Much work is currently underway to model the impacts of human interventions versus natural adaptation and traditional management practices in specific reef regions. Other models have been used to assess efficacy of alternative spatial management strategies. For example, McManus et al. (2021) found regional differences in coral reef persistence across reef networks in the Caribbean, the Southwest Pacific, and the Coral Triangle, depending on ecology, evolution, and habitat network characteristics. Results also suggest that policies that maintain genetic diversity are likely to have important long-term benefits, and thus developing ways to incorporate eco-evolutionary processes into regional-scale conservation planning will be important for mitigating coral loss and facilitating recovery of corals around the world, both during and after warming (McManus et al. 2021).

While these models are constructed to include processes that are supported by empirical data, they are limited by considerable uncertainties surrounding the genetic diversity of different coral species and populations, the genetic architecture of heat tolerance, genotype-phenotype mapping, and gene flow patterns, among others. These models also necessarily abstract other potentially relevant phenomena such as diseases, storms or predator outbreaks, and results should always be interpreted within the context of the unique assumptions and simplifications associated with each model. Specifically, strengthening the application of these approaches to conservation will require addressing the current uncertainty surrounding model assumptions regarding (1) relationships describing climate stressors and critical coral processes such as growth, reproduction, and mortality; (2) measures of genetic diversity in the coral animal and symbionts that underlie the strength of evolution. Empirical studies that address these uncertainties and their interactions will be critical to improve the predictive ability of eco-evolutionary models (see also Box 3).



Percentage of 'healthy' reef cells in three RCP emissions scenarios, with and without adaptation. Model trajectories are shown with no adaptation (black), symbiont shuffling with a +1C advantage (red), symbiont evolution (blue), or combined shuffling and evolution (purple). Panels indicate the three CMIP5 RCP scenarios, RCP 2.6 (a), RCP 4.5 (b) or RCP 8.5 (c). Adapted from Logan et al. (2021).

Defining coral sanctuaries: the 50 Reefs approach

Mass bleaching events in 1983 and 1998 provoked early science on the impacts and theories of climate-change stress responses on coral reefs. Scientific explanations for these events and the production of metrics for their prediction were initiated between 1994 and 2000 (Figure A2). The hotspot and DHWs described above quickly became the primary explanatory variables for thermal-stress events, as these metrics integrated elements of chronic and acute stress. Early investigators realized that coral responses were modified by a variety of common factors, such as light penetration, depth, taxa, and duration of exposure. These were often seen as modifying factors that were of local concern but less amenable to modeling and predictions at larger regional or global scales. However, some of these modifying variables were available from satellites and successfully included at regional and global scales (Maina et al. 2011). The popular adoption of hotspot and DHW metrics lead to the development of 'threshold models' (TM), typified by one or a few synthetic metrics that may or may not include adaptation of corals over time. An additional set of studies and models developed to include variable exposure and other modifying variables, which we term 'variability models' (VM) and typically used more metrics that varied with each investigation, depending on the availability of metrics and the theory and choices preferred by the investigators (Table 1). These two investigative pathways have since dominated the scientific literature (Figure A3).

Both types of models (i.e., threshold and variability) have different abilities to predict bleaching and coral cover that may be changing over time as corals respond to changing exposure (McClanahan et al. 2020a). However, many studies have not used statistical approaches to select the most important variables or other processes to eliminate weak or non-significant variables. For example, only 11% of the threshold model studies used a process of variable selection when developing statistical models compared with 43% of the variability model studies (Table 2). This discrepancy can result in an uncritical acceptance of variables and reduce the rate of learning about stress exposure and its effects on coral reef responses to climate change.

Empirical studies of large-scale patterns in coral cover suggest weaknesses with threshold model approaches. Most critical is that highly influential environmental variables are excluded and therefore coral cover is poorly predicted (McClanahan and Azali 2021). For example, two large compilations of coral cover in Indonesia and the Indian Ocean have shown that non-thermal variables are more important than excess heat for predicting coral cover, namely calcium carbonate (Balch et al 2005) and dissolved oxygen concentrations (Vercammen et al. 2019; McClanahan and Azali 2021). How these variables are changing with climate change and the consequence for coral reefs is largely unknown. Additionally, excess thermal stress is often found to be less important than some other proxies of chronic and acute thermal stress. Rather, it is the excess heat within the context of acute and chronic stresses that matters most (McClanahan et al. 2020a, b; Donovan et al. 2021).

Large data compilations are also suggesting that the state of reefs is and will not be as bad as previously predicted by threshold models (Darling et al. 2019). Findings further suggest acute-chronic stress variables may perform considerably better than models based on DHWs (Vercammen et al. 2019; McClanahan and Azali 2021). The implication of these large coral compilation studies is that contemporary excess-heat models that rely on DHWs may lack the ability to predict coral cover by missing the important aspect of acclimation and adaptation that will be most critical to future states (see Box 1).

Models predicting climate-change refugia, or 'sanctuaries', have been influential in setting priorities for coral reef conservation (e.g., Maina et al. 2011; Beyer et al. 2018). For example, the

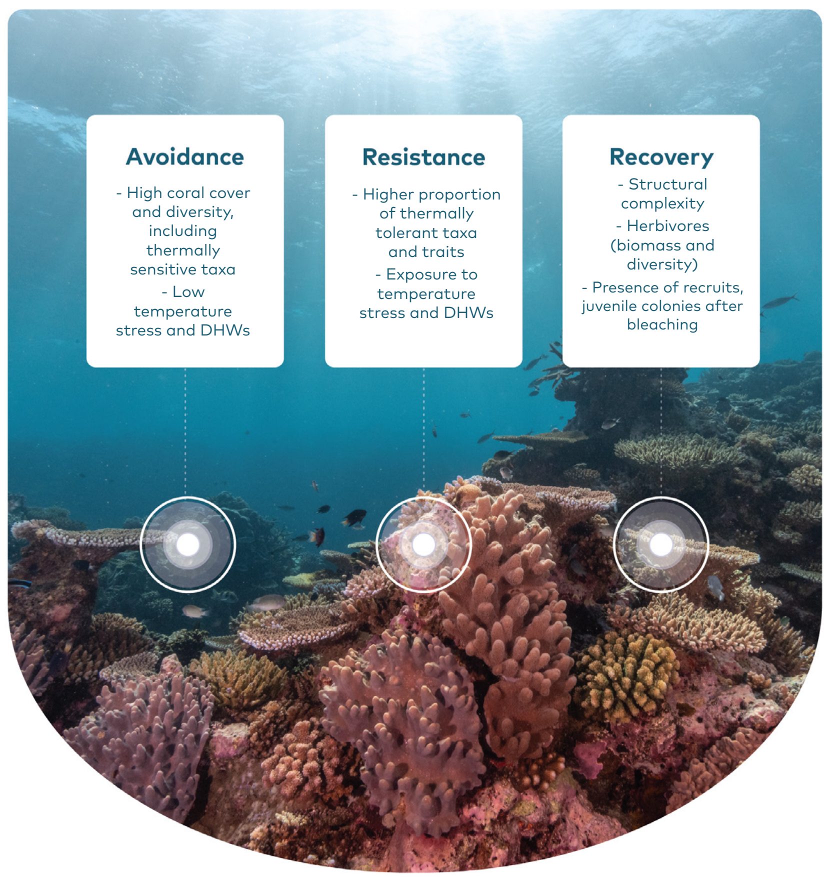


***Figure 1**. Conceptual model of three types of coral sanctuaries, and the characteristics of avoidance, resistance, and recovery sanctuaries.*

50 Reefs study selected exposure metrics within a threshold model framework (excess heat, cyclones, and reef connectivity) to identify a global portfolio of sites expected to persist into the relatively more stable conditions of a successful Paris Agreement (Beyer et al. 2018). For example, 23 of the 30 variables used in the model are highly correlated variations of the hotspot or cumulative excess heat metric, however these metrics can perform weakly in predicting both bleaching and coral cover at larger scales (McClanahan et al. 2015; 2019; McClanahan and Azali 2021). Several large-scale and replicated tests of the relationship between DHWs and coral cover suggest that corals have not declined predictively with cumulative excess heat (i.e., Darling et al. 2019; McClanahan et al. 2020a,b; McClanahan and Azali 2021) and that maximum coral cover can be found at intermediate levels of excess heat (Figure 2b).

If maximizing coral cover is one of the objectives of management, there is a need to reconsider the current usage of the excess-heat theory and what the current selection criteria has identified as sanctuaries. For example, modeling approaches suggest that many reefs with moderate to high cumulative excess heat are 'collapsed' (Obura et al. 2021) and that the safe havens for coral reefs may be almost non-existent at 1.5°C of global warming (Dixon et al. 2022). Yet many contemporary reefs have been shown to have high and persistent coral cover, often composed of communities with mixed coral taxa and functional traits (Darling et al. 2019; McClanahan et al. 2020a,b; Obura et al. 2020; Vercammen et al. 2019; McClanahan and Azali 2021; for more detail see Figure A1). These contrasting interpretations highlight the need to continue to test future predictions with empirical coral reef observations (e.g., contemporary and historical warm conditions in the geological past), and to ensure future predictions integrate the strengths of both threshold and variability models when predicting future climate refugia for coral reefs.

Resistant corals and resistant locations may be particularly underrepresented in the current 50 Reefs portfolio as the 50 Reefs model selected locations where excess heat and cyclone frequency variables were minimized and reefs were potentially connected to promote recovery. Consequently, the sanctuaries chosen are expected to be strongly skewed towards avoidance and recovery conditions, and resistant taxa or sanctuaries will be missed by this approach. In addition, the original 50 Reefs approach can be improved to include coral adaptive capacity (Box 1). Ultimately, predictions of sanctuary theories should be tested with empirical field data and evolutionary models, which can help understand how well they predict intended outcomes (i.e., coral cover, diversity, and reef functioning; Box 2). For example, how well are high coral cover locations represented in the current portfolio? Is this high coral cover associated with specific coral taxa or functional traits and therefore protecting key species? Is the current portfolio over-selecting low exposure, avoidance sanctuaries that may be highly susceptible to catastrophic change when rare thermal stress occurs? How does the theory, metrics, and selection criteria need to change to improve the accuracy of predictions? Would a portfolio that better balances avoidance, resistance and recovery sanctuaries provide more global resilience to climate change? These questions need answers to improve on future phases of sanctuary policies and application. In addition, future models that include local environment variability, hydrodynamics, evolutionary metrics, and water chemistry, and other ecological, social, and governance metrics and contexts could be critical to the successful prioritization and implementation of management interventions.

Box 2 | **WHAT TO MONITOR?**

A holistic and global portfolio of avoidance, resistance and recovery sanctuaries requires identifying locations of high coral cover, high diversity, and high adaptation potential across multiple scales. For example, climate refuges for coral reefs are expected to have: moderate to high coral cover (i.e., >25% cover and mixed taxa), higher rates of coral recovery after climate disturbances, more stress-tolerant taxa taxa, and moderate to high genetic diversity, as compared with non-refuge locations. This requires collaborative efforts to collect data to compile robust, standardized and comparable empirical datasets of:

- Coral cover and community composition;
- Bleaching resistance and recovery;
- Community composition of hard coral taxa and colony size;
- Standing genetic diversity, including habitat diversity and thermal regimes as a proxy for genetic variation.

There is a need to continue to support and strengthen connections between efforts such as the Global Coral Reef Monitoring Network, MERMAID, the Allen Coral Atlas, Reef Cloud, and other community science efforts can leverage substantial existing efforts towards global models to test, improve and predict future climate refuges for coral reefs.

Adding to the 50 Reefs

To illustrate that potential locations of climate refuges could be incorporated in future portfolio efforts, we evaluated the spatial predictions of coral sanctuaries from 15 studies published between 2003 and 2021 (see details in Table A3). We identified each study as threshold models or variability models from the multivariate cluster analysis (Figure A3). Compiling and mapping sanctuaries illustrates the potential for coral reef sanctuaries outside the current 50 Reefs portfolio (Figure 2). This, of course, was expected since the 50 Reefs was the result of a prioritization approach that aimed to protect well connected excess heat refugia. However, this model excluded ecological factors considered important and included in other studies, suggesting (not surprisingly) that the choice of variables used in the modeling approaches influenced the locations of predicted refugia (Figure 2).

These findings suggest the 50 Reef sanctuaries may be only a subset of a much larger set of locations that could be selected for sanctuaries. Therefore, additional criteria such as adding ecological specificity will affect portfolio selection, and future prioritizations with updated information can improve our predictions of additional climate sanctuary locations to add to the 50 Reefs. For example, the 50 Reefs prioritize well connected avoidance sanctuaries and therefore focusing future efforts on resistance and recovery sanctuaries can help identify additional key locations (Figure 3; Table 3). Ultimately, the high potential coverage of sanctuaries globally using these 15 mapped studies is either a hopeful view of the future of coral reefs (compared with Obura et al. 2021, Dixon et al. 2022), or one that suggests a need to be more critical of the metrics being used in models to predict the future state of coral reefs. Given the poor and declining state of many aspects of coral reefs globally, there are clearly several metrics and models that are making poor predictions, or local management is failing to support healthy reefs in these climate sanctuaries.

We have two key suggestions for expanding the 50 Reefs approach:

1. **Add more regional priorities to an expanded 50 Reefs portfolio** (Box 3). For example, Maina et al. (2011) selected locations within [each ecoregion of coral reefs](), as these biogeographical units vary in their ecological and evolutionary history, and subsequently coral sensitivity to climate exposure. Ensuring that sanctuaries are selected within each ecoregion can account for substantial ecoregional differences in coral sensitivity to bleaching and climate change potential shaped by evolutionary history (McClanahan et al. 2020b). Thus, models that choose the lowest stress reefs within each ecoregion ensures a globally distributed portfolio of avoidance sanctuaries such that no ecoregions are excluded from selection. This approach is more inclusive of coral biogeography but is biased towards ‘avoidance sanctuaries’, and suggests a continued focus on regional efforts to prioritize climate refugia (Box 2).

2. **Include resistance and recovery sanctuaries**. Identifying locations of high coral cover, diversity and adaptive potential can add to the existing portfolio of avoidance refuges and require collaborative data efforts globally to compile robust, standardized and comparable empirical datasets. Additionally, niche models can help predict coral species responses to changes in the distribution of environmental variables with climate change (Cacciapaglia and van Woesik 2015, 2016), and could be a proxy for resistance and recovery sanctuaries. Niche models assume that coral distributions are driven by the hard limits to species survival (e.g., a fundamental niche) of temperature, light, calcium carbonate concentration, dissolved oxygen; variables that could be added to future 50 Reefs prioritizations to improve representation.

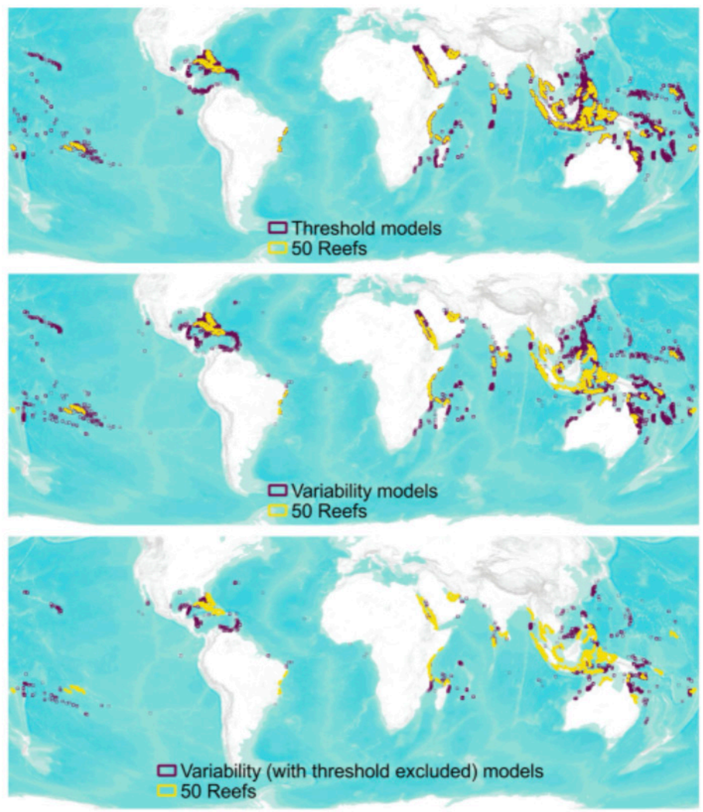
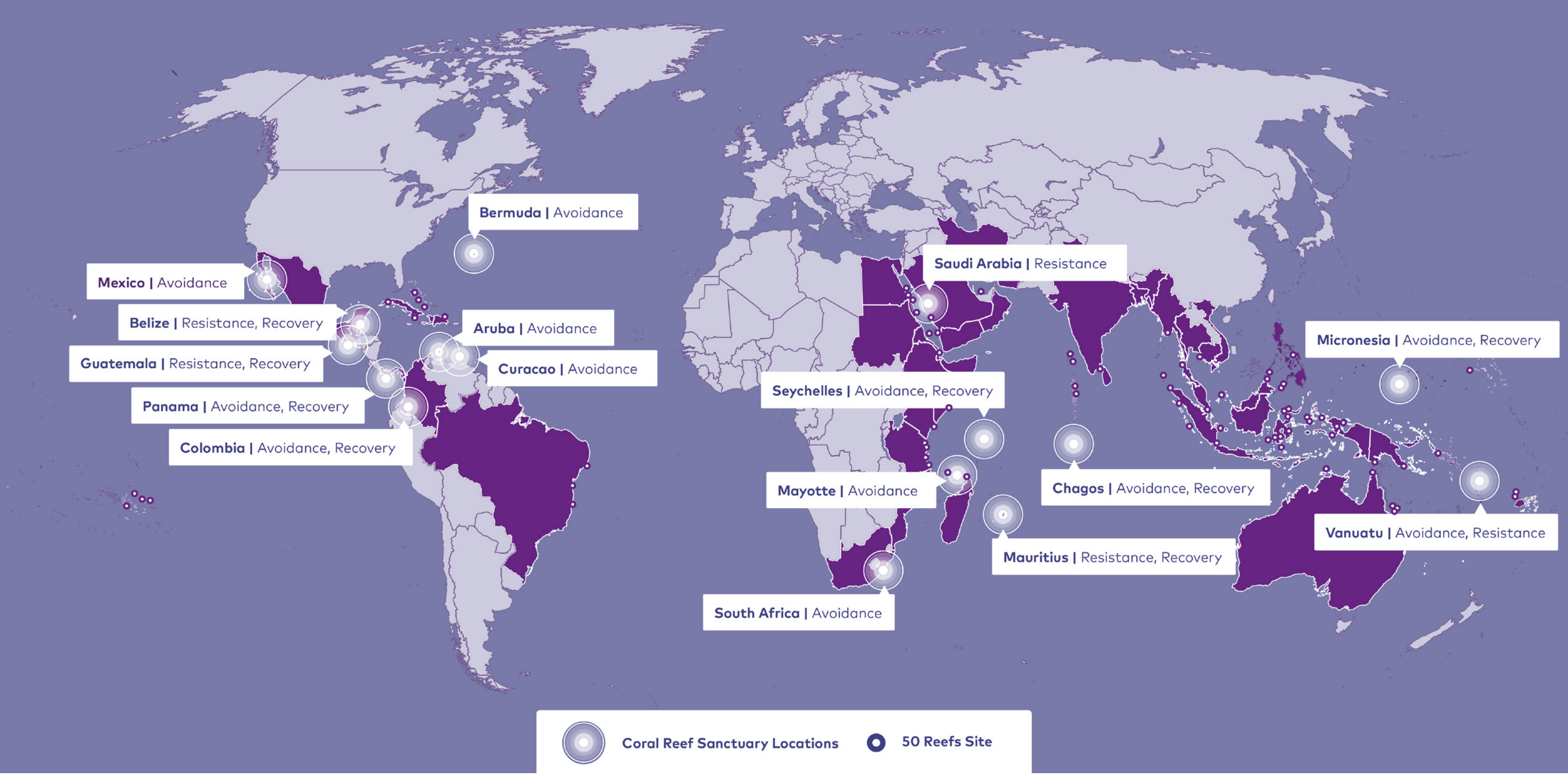


***Figure 2**. Substantial locations of climate sanctuaries might be found outside the existing 50 Reefs locations, shown by mapping 15 published studies of climate sanctuaries for coral reefs (Table A3). Locations of climate refugia (low thermal stress; purple areas) are shown by studies using threshold models (top panel), variability models (middle panel), and variability-and threshold-excluded models (bottom panel) compared to the 50 Reefs analysis (yellow areas; Beyer et al. 2018). Additional locations of climate refuges suggest opportunities to integrate regional prioritizations and resistance/recovery sanctuaries into future portfolio approaches.*

***Figure 3**. Locations of potential avoidance, resistance, and recovery sanctuaries outside of the current 50 Reefs portfolio. More details provided in Table A4.*



Sanctuary models: a way forward

We suggest several options for improving predictions of coral reef sanctuaries to climate change. First, the models need to be compared with each other and tested with empirical surveys of coral cover and community composition to determine which models are making better predictions for variables of interest: coral cover, community composition, and ecosystem functioning (e.g., carbonate production and fish biomass). This will allow for the selection of the best models and will lead to improved models as influential variables are discovered and included while less influential variables are excluded from the models. The variable selection approach has produced a considerable diversity of exposure factors among the 112 exposure papers examined (Table A2). Moreover, most of these studies have evaluated coral bleaching with a smaller subset evaluating coral cover; even fewer have examined coral life histories (Darling et al. 2019) or ecosystem functioning (e.g., Perry et al. 2018).

A remaining question is whether bleaching is the most important response variable for coral reefs, or are there other variables of equal or greater concern, such as community structure, or numbers of taxa, and reef fish diversity or productivity? As coral bleaching is an immediate response to thermal stress rather than an ecological outcome, it is likely that other responses, such as coral cover, growth, recovery rates, or some aspect of the coral community, will be better proxies for the key ecological services of coral reefs. Furthermore, efforts to directly address more important ecosystem services, such as carbonate production, reef growth and biodiversity are missing and yet desirable. Therefore, identifying the most predictive metrics relative to key response variables is a high priority to improve global predictions of coral reef sanctuaries.

Another issue arising from competing models is that the past predictions may be poor at predicting the future. In fact, this is a well-known statistical observation that any prediction of the future will be worse than statistical predictions of the past. For example, a variability modeling approach by Maina et al. (2011) was good at predicting coral cover immediately after the 1998 bleaching event but its ability declined thereafter and in many recent attempts (McClanahan et al. 2015, 2020; McClanahan and Azali 2021). One explanation is that this avoidance model parameterized after the 1998 bleaching event lost its predictive ability as avoidance sanctuaries declined with the “relentless march of mass coral bleaching” (Skirving et al. 2019). Another option is to diversify the types of models from largely avoidance to resistance and recovery sanctuaries. While this diversification of models and sanctuary types may not improve the predictive ability of specific models, it should create a broader portfolio that reduces decision failures by spreading risks when future outcomes of specific models are poorly known (Webster et al. 2017).

A second option is to create ensemble models of sanctuary prediction to address future uncertainty, whereby priority locations need to be identified as sanctuaries by multiple models. This multi-model approach is often used in climate modeling and results in improved predictions of future states. If, for example, several models predict the same location for sanctuaries, then these common 'no regrets' locations should be higher priorities for conservation investment. The process of variable and model selection included do, however, need to pass some thresholds and have some predictive power. That is, from the above competition of models, there are likely to be models that will not pass these thresholds, or be weakly predictive, and fail when compared with other models. Weak predictive variables and weak models can be dropped from the portfolio of models that are then used to make predictions, and the variables can be revisited thereafter to determine if they still have weak predictive capacity. Towards developing a truly robust portfolio, each model should be based on different assumptions, variable choices, and variable weights. That is, if models are strongly autocorrelated in their assumptions, variable selection, and predictions, the inclusion of a group of similar models may not produce the desired robustness. This may seem like a challenging task, but it is an approach used by the global community of climate modelers and is required to avoid overreliance on specific, over-fit, and weak models. Furthermore, including geological indicators or variables from physical climate theory could also be applied to future sanctuary models, in addition to ecological or environmental variables.

A recent study indicated that comparing fundamentally different models and searching for positive coincidence in sanctuaries is possible (McClanahan and Azali 2021; Figure A4). This study used a large dataset of coral cover field surveys from the Western Indian Ocean to compare and compete models with each other using the same field data under different climate change scenarios. In this study, a variability model identified seven significant variables and showed that threshold variables were among the weakest options (i.e., not significant). While sanctuaries (i.e., >25% coral cover in 2050) were predicted by both models (Figure A4), the variability model predicted a far larger number of sanctuaries than the threshold model. In addition, the variability model selected fisheries management as a significant variable and that increasing fisheries restrictions in the region considerably improved the predicted coral cover of reefs in 2050. Consequently, this early effort to compare models suggests a need to reconsider and expand the 50 Reefs portfolio using other model options.

Box 3 | LOCAL AND REGIONAL APPROACHES TO IMPLEMENTING A PORTFOLIO OF RESILIENT REEFS

Models, particularly at the global scale, are inherently imperfect representations of the world. The choice of variables used in global coral reef stress models is necessarily constrained by data availability. Many types of climate and oceanographic data are acquired from remote sensors across larger pixel sizes (from hundreds of meters to kilometers) that integrate conditions across much larger spatial scales than the localized environmental parameters driving coral reef response (Jupiter et al. 2013). Additionally, critical social-economic factors to conservation planning such as culture, governance or political will do not exist at the global scale and are therefore excluded from prioritization efforts. These dual challenges affect both model performance and subsequent implementation, through mismatches in timing or scale of environmental parameters that influence coral response or omissions of potentially critical social-economic factors.

One approach to improving global models is to downscale to regional levels, where finer-scale spatial and temporal data can better account for more localized atmospheric and oceanographic conditions (e.g., island effects). Local and regional models also offer the opportunity to integrate data on other non-thermal stress impacts, such as land-based runoff, fisheries management/dependency, or resource use/governance that may not be available at high enough resolutions at the global scale or available via expert opinion. Notably, these efforts can find more hopeful outcomes for the persistence of coral reefs under climate mitigation and fisheries management (McClanahan and Azali 2021; Figure A4). For example, efforts are underway to downscale the 50 Reefs assessment regional and national rankings of coral climate refugia for 5,000 ha of priority coral reef ecosystems in Cuba, Dominican Republic, Haiti & Jamaica (TNC Coral Climate Refugia, Chollett et al. in press).

Regional models can also suffer the same mismatches of scale between satellite-derived thermal impacts, in situ temperature conditions and coral communities, and governance contexts triggering response. The uncertainty in global and regional presents some concern when model outputs are used within decision-support algorithms to identify portfolios for investments in resilient reefs. Therefore, the outputs of decision-support tools should always be the beginning of conversations with key stakeholders (e.g., practitioners, rights holders, government agencies) about potential investable opportunities. These opportunities can be then better refined with local field data, particularly time series data that demonstrate aspects of resilience (e.g., stress tolerance, high coral cover despite multiple disturbances, rapid recovery, etc.).

Decisions about financing must also consider social-cultural enabling conditions, especially governance quality and capacity to promote positive coral reef management outcomes. One pathway forward is to invest in regional funds that can support the management of coral reefs (e.g., Micronesia Conservation Trust, the Caribbean Biodiversity Fund, or other trust funds; Victurine et al. 2022). These regional funds, through scientific steering committees, could set evaluation criteria requiring demonstration of evidence from model outputs, field data, and local consultation about why a particular reef area would fall into any of one of the three categories of reef sanctuaries (i.e., avoidance, resistance, recovery). Critically, each proposal should be required to demonstrate some political will at the site level to engage in management implementation, as well as capacity for management to yield returns. Selection and evaluation of sites across a portfolio of avoidance, resistance, and recovery sanctuaries can provide important learning through active adaptive management (Grantham et al. 2010), which will improve the likelihood that future investments are targeted to the most resilient reefs.

The future of climate sanctuaries for coral reefs

A fundamental concern for all reef stakeholders is the consequences of climate change on the state of reef growth and fisheries (Perry et al. 2020). Can community composition or functional biological traits help evaluate the three types of refugia? Should conservation efforts focus on avoidance sanctuaries and specific taxa that largely represent a few traits such as fast recovery and dominance by a few taxa, or both? Are these avoidance and recovery sanctuary types preferable to a more diversified set of taxa that might contain an abundance of stress resistant taxa and a resistance sanctuary? What are the consequences of each for reef growth and fisheries production? Answers to these core questions will enable us to better define conservation objectives.

Ongoing changes in coral communities are expected to have consequences for reef services but remain currently poorly understood. And yet, decisions have been and will continue to be made in the absence of this knowledge. Here, we outline an approach to conserve and utilize this diversity to better understand the consequences of these decisions. That is, reduce the number of presumptive decisions about preferred sanctuaries prior to a fuller understanding of the consequences of this variation for future human services. The new priorities should promote a more diversified and learning-based approach to sanctuaries.

There are several efforts to collect reef data on large scales, including the Global Coral Reef Monitoring Network, Reef Check, MERMAID, Reef Cloud, Allen Coral Atlas, and other community science efforts. However, in many cases, the efforts to analyze these data are ad hoc and often dependent on the interests of academics. Additionally, they are often evaluating the coral stress responses rather than the processes that lead to the three types of sanctuaries. Low stress response and sanctuaries are too often assumed to be synonymous but, as described above, they are not. There are a whole series of mitigating circumstances that include, for example, episodic variability, diseases, land-sea interactions, dispersal, and meta-population dynamics. Many new and important variables have been recognized but many are not being modeled. Climate future projection projects, such CMIP, need to diversify their modeled variables beyond temperature and excess heat to include variables that have been shown to predict coral reef responses, such as calcium carbonate concentrations, dissolved oxygen, nutrients, or genetic variability, among others.

Often critical but poorly overlooked is the governance context and the ability and willingness of people to effectively engage in solutions (Box 3). No amount of science can overcome a social inertia to not act or to act in short-term selfinterest rather than the long-term protection of critical resources. For example, some nations in the current 50 Reefs portfolio have long histories of poor outcomes of protected area management and widespread use of destructive fishing (McClanahan et al. 2006, 2015; Hampton-Smith et al. 2021). Short-term production of food, often at the expense of long-term sustainability, marks the policies of many but not all tropical nations. Countries with long histories of autocratic governance are often associated with a weak history of supporting conservation without external support (McClanahan and Rankin 2016). Governance policies that subsidize extraction rather than invest in the defense of natural resources are likely to increase both human and natural resource poverty (McClanahan and Kosgei 2017). Future efforts may be better served by considering enabling conditions, such as political will, feasibility, and cost-benefit of management based on historical success rates of various resource management efforts or new opportunities for conservation support (Jones et al. 2018).

Any effort to make good predictions is going to require the principles of continuous learning. That is, both exploratory and adaptive science that is closely tied to adaptive management. The task is too large for any single set of investigators but requires a learning community and platform that extends the normal bounds of academic and conservation NGO research. Future scientific efforts for the 50 Reefs need to encourage and support diverse approaches and avoid the pitfall of seductive theories. At the same time, future efforts must be prepared to learn and adapt as global and local stressors create novel and challenging conditions for coral persistence. This will require acknowledging and learning from failures while recognizing the constraints of limited time and resources for coral reef conservation. Furthermore, future 50 Reefs efforts must be continually trialling and updating information, combining empirical surveys and environmental remote sensing information, and working closely with reef managers, stakeholders, scientists and funders to develop critical conservation priorities for coral reefs from local to regional to global scales.

Conclusions

Drawing on 30 years of scientific studies of climate impacts and refugia for coral reefs, we outline several ways that the science of coral reef sanctuaries can be improved, and suggest new approaches to identify potential climate refugia based on a holistic consideration of avoidance, resistance and recovery sanctuaries. First, models should consider a more diversified group of exposure and response variables. By using local knowledge, models at finer geographic resolution can also be developed where global level data are lacking or poor indicators of reef status. The response variables should be expanded to include those most critical for a suite of ecosystem services rather than relying largely on coral responses to thermal exposure. These diversification measures will increase the chances of including additional sanctuaries that fall within the resistance and recovery sanctuary categories. Moreover, sanctuary models should evolve over time as coral reef monitoring couples with the increased availability and resolution of environmental exposure data and artificial intelligence or machine learning algorithms. Developing a standardized and globally comparable monitoring dataset can facilitate an adaptive science program that continuously improves predictions for identifying sanctuaries.

Based on information in 30 reviewed sanctuary studies, many reefs may be potential additions to the existing portfolio of 50 Reefs (Figure 2 and 3; Table A3). There are also empirical compilations of field data that show where the highest coral cover is located (Darling et al. 2019). Very simple models that, for example, have identified high coral cover in sites with intermediate excess heat and modest efforts can be used to scale up this approach globally. It is now feasible to create improved site-identification models using variables beyond excess heat to improve selections for climate refugia. Overall, combining field data and observations, multiple exposure variables, and artificial intelligence/machine learning can improve early modeling science to become a more accurate predictive set of ensemble models similar to climate predictions used by the Intergovernmental Panel on Climate Change (IPCC). For a full suite of technical recommendations, see Annex 2.

Recommendations

→ The review indicates that there are a number metrics that can identify avoidance sanctuaries that can provide a broader foundation for coral reef conservation than currently practiced.

→ New investments to further identify, evaluate, and protect areas of coral resistance and recovery will stimulate learning through adaptive management. The result will be more confidence in the selection process and ensure a broader portfolio of priority locations to develop a robust portfolio for the survival of tropical coral reefs.

→ Increase support for regional downscaled portfolios of sanctuaries that can better characterize local climate conditions, regionally important data on other non-climate human pressures, and social-economic knowledge of resource use, governance, and political will. Investments in regional trust funds or impact investing (e.g., Micronesia Conservation Trust, the Caribbean Biodiversity Fund; Victurine et al. 2022) supported by scientific advisory boards can provide this expertise for synthesizing regional model outputs, field data, and processes of local consultation.

→ Strengthen large-scale data-driven coral reef monitoring efforts that provide high-resolution and near real-time information on benthic communities and reef fish assemblages at global scales in order to test and develop new models and predictions of climate sanctuaries.

→ As the impacts of climate change accelerate and push reefs towards novel responses, continue to evaluate and update investment priorities in parallel with the latest climate coral reef science. ■

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