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Conservation Biology

REVIEW

Diversification of refugia types needed to secure the future of coral reefs subject to climate change

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Abstract

Identifying locations of refugia from the thermal stresses of climate change for coral reefs and better managing them is one of the key recommendations for climate change adaptation. We review and summarize approximately 30 years of applied research focused on identifying climate refugia to prioritize the conservation actions for coral reefs under rapid climate change. We found that currently proposed climate refugia and the locations predicted to avoid future coral losses are highly reliant on excess heat metrics, such as degree heating weeks. However, many existing alternative environmental, ecological, and life-history variables could be used to identify other types of refugia that lead to the desired diversified portfolio for coral reef conservation. To improve conservation priorities for coral reefs, there is a need to evaluate and validate the predictions of climate refugia with long-term field data on coral abundance, diversity, and functioning. There is also the need to identify and safeguard locations displaying resistance toprolonged exposure to heat waves and the ability to recover quickly after thermal exposure. We recommend using more metrics to identify a portfolio of potential refugia sites for coral reefs that can avoid, resist, and recover from exposure to high ocean temperatures and the consequences of climate change, thereby shifting past efforts focused on avoidance to a diversified risk-spreading portfolio that can be used to improve strategic coral reef conservation in a rapidly warming climate.

KEYWORDS
climate change, coral reefs, environmental stress, gap analysis, marine spatial planning, refugia

Diversificación de los tipos de refugio necesarios para asegurar el futuro de los arrecifes de coral sujetos al cambio climático

Resumen: Una de las principales recomendaciones para la adaptación al cambio climático es identificar los refugios de los arrecifes de coral frente al estrés térmico del cambio climático y mejorar su gestión. Revisamos y resumimos ∼30 años de investigación aplicada centrada en la identificación de refugios climáticos para priorizar las acciones de conservación de los arrecifes de coral bajo un rápido cambio climático. Descubrimos que los refugios climáticos propuestos actualmente y las ubicaciones que pueden evitarlos dependen en gran medida de métricas de exceso de calor, como las semanas de calentamiento en grados (SCG). Sin embargo, existen muchas variables alternativas de historia vital, ambientales y ecológicas que podrían utilizarse para identificar otros tipos de refugios que resulten en el acervo diversificado que se desea para la conservación de los arrecifes de coral. Para mejorar las prioridades de conservación de los arrecifes de coral, es necesario evaluar y validar las predicciones sobre refugios climáticos con datos de campo a largo plazo sobre abundancia, diversidad y funcionamiento de los corales. También es necesario identificar y salvaguardar lugares que muestren resistencia a la exposición climática prolongada a olas de calor y la capacidad de recuperarse rápidamente tras la exposición térmica. Recomendamos utilizar más métricas para identificar un acervo de posibles lugares de refugio para los arrecifes de coral que puedan evitar, resistir y recuperarse de la exposición a las altas temperaturas oceánicas y las consecuencias del cambio climático, para así desplazar los esfuerzos pasados centrados en la evitación hacia un acervo diversificado de riesgos que pueda utilizarse para mejorar la conservación estratégica de los arrecifes de coral en un clima que se calienta rápidamente.

PALABRAS CLAVE
análisis de brecha, arrecifes de coral, cambio climático, estrés ambiental, planeación espacial marina, refugios

需要多样化的避难所来保障受气候变化影响的珊瑚礁的未来

【摘要】识别保护珊瑚礁免受气候变化热胁迫影响的避难所并加强其管理是气候变化适应的重要建议之一。我们回顾和总结了约30年来关注如何确定气候避难所来优先保护受快速气候变化影响的珊瑚礁的应用研究。我们发现, 目前提出的气候避难所及可以避开气候变化影响的地点高度依赖于衡量过多热量的指标, 如周热度。然而, 还存在许多替代性的环境、生态和生活史变量, 可用于确定其他类型的避难所, 它们可以提供珊瑚礁保护所需的多样化组合。为了改进珊瑚礁的优先保护决策, 需要用珊瑚丰度、多样性和功能的长期野外数据来评估和验证对气候避难所的预测。还需要识别和保护表现出气候抵抗力的地点, 即长期暴露在热浪中且在热暴露后能够迅速恢复的地点。我们建议使用更多指标, 为珊瑚礁确定潜在的避难所组合, 帮助珊瑚礁避免和抵抗海洋高温暴露和气候变化的影响, 并得到更好的恢复, 从而将过去专注于避免海洋高温暴露的努力转变为多样化的风险分散组合, 来促进快速气候变暖下的珊瑚礁战略保护。**【翻译:胡怡思;审校:聂永刚】**

关键词: 气候变化, 环境压力, 空缺分析, 海洋空间规划, 避难所, 珊瑚礁

INTRODUCTION

Coral reefs have complex ecological, evolutionary, and geological histories (Dubinsky & Stambler, 2010). These histories have created a diversity of habitats, species, and emergent reef communities with variable responses to environmental change. As climate change provokes rapid, intensive, and large-scale impacts to coral reefs, there are some historical prece-

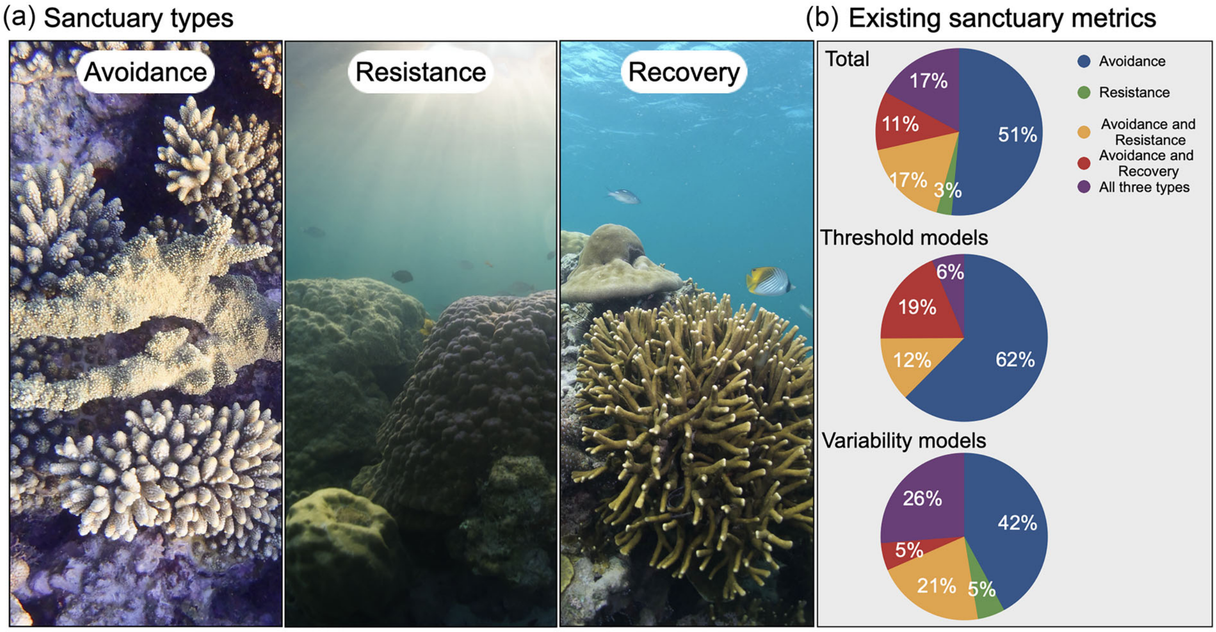

FIGURE 1 (a) Three main types of climate refugia characterized by unique environments and associated taxa that represent variable coral life histories and community organization responses to climate change: (left) avoidance refugia, locations that avoid physical exposures; (middle) resistance, locations have low sensitivity to climate change; and (right) recovery locations can recover quickly after exposure. (b) Classification of the 35 published studies showing the percentages identified using metrics that fall within the 5 possible coral reef refuge categories.

dents that indicate the possibility of considerable adaptation (Pandolfi et al., 2011). For example, reef communities often show predictable changes and adaptation to stress across reef zones, along inshore to offshore gradients, from windward to leeward sides of islands, across archipelagos, across seasons, and along large ocean–basin geographic gradients (Asner et al., 2022; Camp et al., 2018; McClanahan, Darling, et al., 2020; McClanahan, Maina, et al., 2020; Selmoni et al., 2020). Therefore, coral reefs are expected to display a variety of responses, as exemplified in the diverse terminology and concepts used to describe outcomes of climate change (Camp, 2022; Kavousi & Keppel, 2018).

Here, we refer to *refugia* as locations where biodiversity retreats to, persists in, and potentially expands from once environmental conditions change (Keppel et al., 2012). Refugia are often based on historical evaluations, but we primarily investigated the environmental and ecological processes that produce refugia. After evaluating the impacts of climate disturbances and the processes that influence thermally stressed corals, West and Salm (2003) recognized 3 major categories of refugia for reefs: avoidance, resistance, and recovery (Figures 1a & 2). Moreover, they and others recognize that this diversity of responses and associated locations creates a potential for strategic conservation science and interventions (Anthony et al., 2020; Camp, 2022; Chollett et al., 2022; Hoegh-Guldberg, Kennedy, et al., 2018; McClanahan & Azali, 2021; McClanahan & Muthiga, 2017; Webster et al., 2017). Therefore, we reviewed the applied work that has evaluated progress toward promoting the diversified portfolio approach recommended to improve the chances for coral adaptation and persistence under rapidly warming ocean conditions.

Ecosystems are vulnerable to collapse when stressed beyond their capacity to adapt. For coral reefs, this collapse is typically associated with coral bleaching and mortality from prolonged exposure to high ocean temperatures that leads to the loss of sensitive coral taxa, large coral colonies, declines in live coral cover, or transitions to noncalcifying macroalgae, sponge, and soft corals (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 capacity of reef species and assemblages to adapt (McManus et al., 2021). Climate change increases the exposure of coral to extreme temperatures, more acidic seawater, and less dissolved oxygen, but the outcomes of this exposure depend on the natural variability and the ability of corals to resist and recover from this exposure (McClanahan & Maina, 2003; Sully et al., 2019; Dixon et al., 2022; Donovan et al., 2021). Environmental exposures can be considered chronic and acute stressors, and in most cases human pressures are aggravating the chronic and accentuating acute exposure (He & Silliman, 2019; Andrello et al., 2022). These interactions have consequences for coral reef species and communities based on their traits and life histories (Darling et al., 2012, 2019), given that some species will be more adapted to different types of disturbances and others more capable of rapidly recovering from disturbances. Coral bleaching, or the breakdown of the coral host and algal symbiosis, results from various environmental exposures and can lead to differential mortality and reorganization of the community. In the context

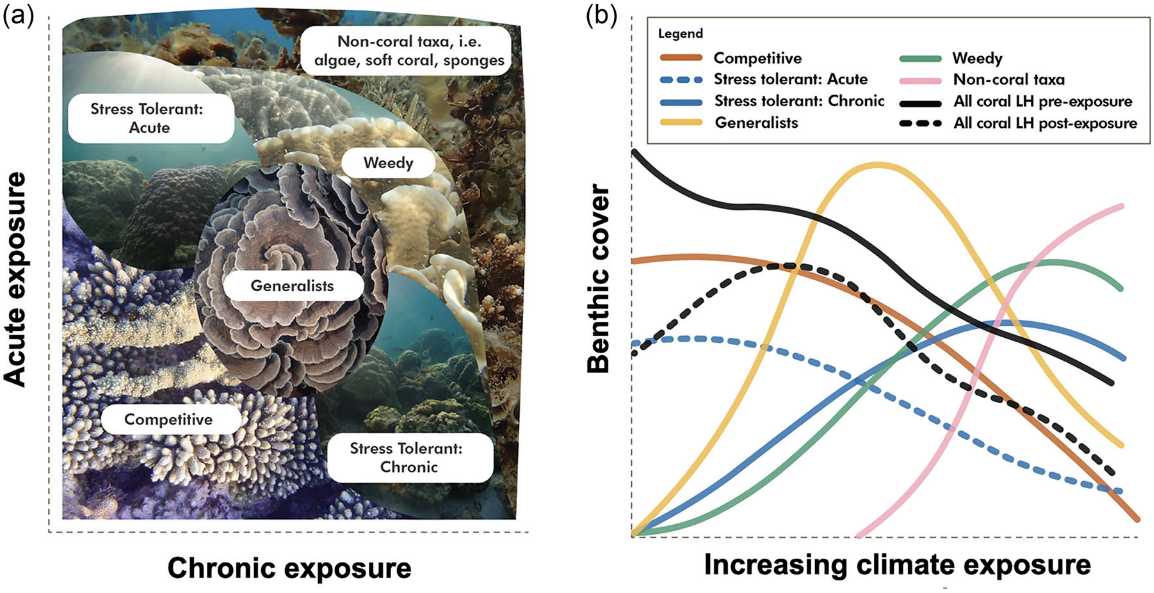

FIGURE 2 (a) A theoretical framework of chronic and acute stresses and the resulting expectations of coral taxa and trait responses or life histories (LH) (Darling et al., 2012) and (b) predictions of benthic cover based on the theoretical framework.

of climate change, prolonged exposure to high ocean temperatures increases the exposure of corals to damaging heat stress that can cause corals to expel their symbiotic algae, leading to the loss of color and ultimately the death of the coral colony. At a community and ecosystem level, bleaching causes biological reorganization that has substantial consequences for ecosystem services that coral reefs provide. These include tourism, fisheries production, and coastal protection that includes protection from sea level rise and more frequent and intense storms (Ferrario et al., 2014; McClanahan et al., 2002).

After a series of global bleaching events, coral reef scientists investigated responses to climate disturbances and developed approaches to define and identify potential refugia (McClanahan, 2022). Here, we define reef *refugia* conservation priorities as locations where characteristics of avoidance, resistance, and recovery provide substantial ecological resilience to climate change and where other nonclimate pressures, such as overfishing, pollution, disease, and dredging, should be urgently mitigated to reduce ecological degradation. Avoidance refugia have stable and cooler water temperatures, resistance refugia have coral assemblages with lower sensitivity to extreme heat and subsequently less bleaching and mortality, and recovery refugia have the ecological capacity to recover after bleaching and mortality. There is abundant evidence that these refugia types vary considerably with geography (Eladawy et al., 2022; Hedouin et al., 2020; McClanahan, Darling, et al., 2020; McClanahan, Maina, et al., 2020; Roff & Mumby, 2012). Ultimately, coral reefs have the best chance to survive and function within these 3 types of refugia when other local pressures are mitigated through good management, such as sustainable fisheries management and pollution reduction. Therefore, we summarized scientific efforts to identify geographic locations and types of coral refugia in order to make recommendations that improve the current science and actions needed for an improved strategy for global coral reef conservation.

CORAL RESPONSES TO CLIMATE DISTURBANCES

Coral responses to acute and chronic disturbances can provide a useful framework to predict impacts of climate change (Chollett et al., 2022). Acute stressors are defined as episodic stresses that may periodically exceed thresholds of optimal or livable conditions specific to the organisms' survival capacity (Figure 2a). For coral reefs, acute thermal stresses are mostly evaluated as short-term deviations from the above warm-season variability or chronic stress. Prolonged exposure to high ocean temperatures is the most frequently evaluated stress on coral reefs and measured relative to a mean summer baseline for the existing satellite-based time series (McClanahan, 2022). Specifically, the metric of degree heating weeks (DHWs) is calculated by multiplying the number of weeks that the water temperature is above an average summer baseline by the number of degrees above the threshold. The threshold temperature at which coral begins to experience stress may vary, but the convention is to use 1 °C above the long-term satellite-derived summer mean. For example, if the temperature is 2 °C above summer average temperatures and remains at that level for 3 weeks, the DHW would be 6 (2 °C × 3 weeks) (Liu et al., 2014). Acute stresses, therefore, largely lie outside the envelope of normal historical environmental conditions. The result is typically coral bleaching and mortality of vulnerable coral species (e.g., branching and plating acroporids [Darling et al., 2013]). The result is a community-level shift to more tolerant coral species that can resist and recover from exposure to acute temperature stress (Loya et al., 2001; McClanahan et al., 2020; Roche et al., 2018). Whether this change is temporary or persistent depends on historical exposure and concordance with past and current disturbance amplitudes and frequencies.

Chronic stress refers to a long-term or ongoing state of environmental stress and exposure relative to baseline conditions. Facing long-term chronic stress, corals can become more tolerant or have adverse response and increased mortality. Chronic stressors include important short-term elements of stress, such as the daily to seasonal changes in tides, light, and temperatures (Figure 2a), and the longer term environmental history of reefs at ecological and evolutionary scales. Short-term acute disturbances interact with long-term chronic stress. For example, long-term ocean oscillations, such as El Niño Southern Oscillation and the Indian Ocean Dipole, can also affect the year-to-year changes in temperature stress experienced by corals (Abram et al., 2020). Thus, the differences between acute and chronic stress can depend on organismal sensitivity and community organization that contains some "memory" induced by past exposure (Hughes et al., 2019). Functional traits and genetics and the frequency of historical exposures may, therefore, influence adaptation potentials. Ultimately, high levels of acute and chronic disturbance will shift coral communities toward smaller colonies and species and less diverse communities (Lachs et al., 2021; McClanahan et al., 2008) and can ultimately shift ecological dominance on coral reefs toward other noncalcifying organisms (Reverter et al., 2022; Robinson et al., 2019). This leads to the losses of refuge for biodiversity and ecosystem functioning, such as reef growth, that is critical for fisheries production and shoreline protection.

Chronic and acute stresses influence species' traits, community organization, and their changes across disturbance events. Therefore, these attributes should be reflected in avoidance, resistance, and recovery refugia, and data on these attributes can be tested against predictions. For example, the 4 possible quadrats of acute and chronic stressor should be reflected in the dominance of different life-history groups: competitive, stress-resistant, ruderal, and generalist taxa (Darling et al., 2012) (Figure 2a). Reefs and refugia types should reflect a mosaic of coral taxa or functional traits that emerged from the interactions between chronic and acute stress (Darling et al., 2019). These traits, community composition, and subsequent refugia types can, in turn, indicate the state of ecosystem service provisions for humans. A diversity of these attributes is expected to provide the functional redundancy and resilience to maintain sustainable services (Reverter et al., 2022). In some cases, however, environmental exposures may simply become too extreme for reefs to be colonized by anything other than noncoral and noncalcifying taxa, with subsequent losses of services.

DEFINING CORAL REFUGIA

Mass bleaching events in 1983 and 1998 provoked the early science on the impacts and theories of climate-change stress responses on coral reefs (McClanahan, 2022). Notably, metrics of thermal hotspots and degree-heating metrics (DHW) quickly became the primary explanatory variables for thermal-stress events because these metrics integrated elements of chronic and acute stress (Liu et al., 2014). Although scientists realized that coral responses were modified by a variety of common factors, such as light penetration, depth, taxa, and duration of exposure (Hughes et al., 2003), these were often seen as modifying factors that were of local concern and less amenable to modeling and predictions at larger regional or global scales. By the early 2010s, satellite and remote sensing provided several modifying variables, including ultraviolet light, currents, and water clarity, that were successfully included at regional- and global-scale evaluations of coral reef bleaching (Maina et al., 2011).

The popular adoption of thermal hotspot and DHW metrics and the scale of the climate models (1° × 1° or 5 × 5 km) led to the development of large-scale threshold models that were developed from global coverage and model predictions of sea surface temperatures (SSTs) to project future bleaching (Heron et al., 2016; Logan et al., 2021). These global threshold models were developed from model predictions of SSTs and used to project future bleaching patterns. Thus, early climate projections were at a very coarse scales of 1° grid cells and monthly SSTs (Donner et al., 2005). An additional set of studies and models often developed at a finer spatial scale included a variety of exposure and modifying variables, such as light, currents, and water quality (McClanahan, 2022). Sometimes they considered the specific responses and niches of coral or specific taxa responses to thermal stress. We pooled these studies and termed them variability models because they typically evaluated the variability contained in continuous metrics. Metrics varied with each investigation, depending on their availability and the investigator's preferred theories and choices. These correlative investigative pathways have since dominated the scientific literature for quantifying reef exposure and identifying refugia (Figure 3). We did not review mechanistic models of thermal stress that largely focus on scales considerably smaller than conservation planning (Kavousi & Keppel, 2018).

Threshold models were primarily developed to predict coral bleaching at large scales. Nevertheless, they are frequently used to infer future states of reefs, including coral cover and recruitment (Cornwall et al., 2021; Sheppard, 2003). Threshold models and environmental variability models have different abilities to predict bleaching and coral cover (McClanahan et al., 2019). However, systematic statistical variable-selection approaches have rarely been applied in threshold model studies, and the predictive strength of thermal and nonthermal stress variables is seldom known. For example, a review of 112 coral–climate impact studies (McClanahan, 2022) showed that only 11% of the threshold model studies used a selection process for statistical variables, compared with 43% of the variability model studies (McClanahan, 2022). To date, identifying refugia relies largely on the satellite-derived environmental variables chosen to detect conditions of prolonged heat exposure that overlook the ability to describe and predict additional areas of coral resistance and recovery following exposure to bleaching conditions.

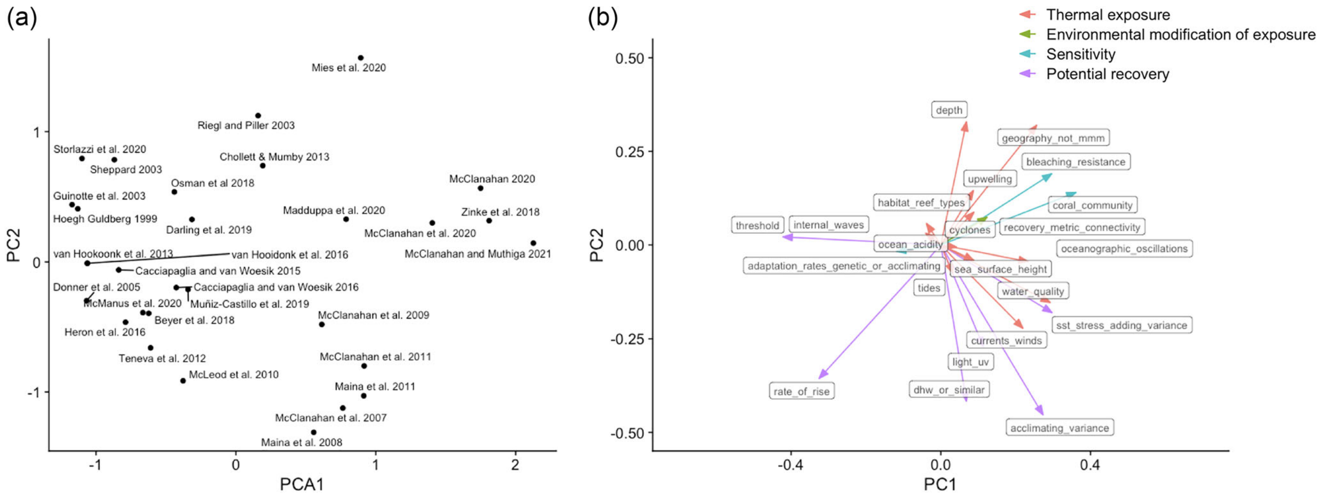

FIGURE 3 Multivariate analysis of studies evaluating climate refugia for coral reefs as per (a) specific publications and (b) variables evaluated by the investigators. The studies were classified prior to the principal component analysis as threshold models if the main metric of analysis was a variable for which excess heat was the summed temperature above a predetermined temperature or as variability models if continuous variables were the main methods of evaluation.

THE PROBLEM

A positive relationship among coral bleaching, mortality, subsequent coral cover, and reef functioning is frequently inferred by climate stress and refugia predictions (Beyer et al., 2018; Cornwall et al., 2021). Yet, threshold metrics of prolonged exposure to excessive heat (typically DHWs) are not among the strongest variables for predicting bleaching, mortality, and coral cover (McClanahan, 2022). Moreover, threshold metrics are frequently modified by several other environmental variables that are seldom included in predictions made by threshold modeling studies. For example, large compilations of coral cover in Indonesia, Indian Ocean, and Southwest Atlantic show that nonthermal variables of dissolved calcium carbonate, oxygen concentrations, and turbidity in seawater are better predictors of coral cover than excess heat (DHWs) (McClanahan & Azali, 2021; Santana et al., 2023; Vercammen et al., 2019). Proxies of chronic and acute thermal stresses often perform better than DHWs when predicting bleaching and coral cover (Donovan et al., 2021; McClanahan & Azali, 2021; McClanahan, Darling, et al., 2020; McClanahan, Maina, et al., 2020; Vercammen et al., 2019). Moreover, several studies show a nonlinear response between temperature exposure and coral cover that suggests complex dynamics of coral adaptation and potential resilience (Darling et al., 2019; McClanahan & Azali et al., 2020; McClanahan, Darling, et al., 2020). The threshold or location of the peak response of coral cover can change with geography and over time, including after repeated bleaching events (DeCarlo, 2020; Shlesinger & van Woesik, 2023). As a result, a key assumption of many threshold modeling studies that coral conditions decline linearly with cumulative exposure gradients simplifies a more complex relationship.

Most people who rely on tropical reefs are worried about the impacts of reef degradation on the ecosystem services they provide. Therefore, a key requirement of strategic coral reef management is to secure the long-term support of coral reef ecosystem services. Although threshold models have been influential in setting priorities for coral reef conservation (Beyer et al., 2018; Maina et al., 2011), they prioritize areas with less future excess heat, fewer cyclones, and more ecological connectivity (Beyer et al., 2018; Chollet et al., 2022). However, 23 of the 30 variables used in 1 global model (Beyer et al., 2018) were highly correlated variations of the thermal hotspot or DHW metrics (McClanahan, unpublished analyses), which suggests an overreliance on a single core metric (DHW) used to identify short-term bleaching impacts. Furthermore, threshold metrics often perform weakly in predicting bleaching and coral cover at larger scales compared with other variables (McClanahan et al., 2015, 2019; Mollica et al., 2019; McClanahan, 2022). For example, many Indian Ocean reefs should have collapsed based on moderate to high cumulative excess heat metrics predictions (Obura et al., 2021; Sheppard, 2003). But, threshold predictions are inconsistent with field data compilations of coral community dynamics that show coral cover increases and recovery, fluctuations, and taxonomic changes in coral assemblages since the late 1980s (McClanahan et al., 2014; Darling et al., 2019; Obura et al., 2020).

On regional to global scales, the ability of the various DHW metrics to predict bleaching rarely exceeds 20% when there is no spatial optimization, and false positives and negatives are excluded from calculations (van Hooidonk & Huber, 2009; DeCarlo, 2020). Accounting for other environmental covariates is likely to reduce this predictive ability further (McClanahan et al., 2019). This suggests modest amounts of excess thermal heat promote coral cover by mechanisms that probably represent an adaptation to the balance between chronic and acute thermal exposure. Ultimately, evaluating the mechanisms of adaption and ecological organization will add more realism to conservation prioritizations.

CHANGING COURSE

Identifying refugia that provide ecosystem services requires reconsideration of the metrics used to identify and classify refugia. Avoidance refugia for coral reef identified by the excess heat models at 1.5 °C of global warming are expected to largely vanish by 2 °C of global warming (Dixon et al., 2022), which can provoke despair and hopelessness for coral reef conservation. Yet, many contemporary studies show reefs have high and persistent coral cover that is often composed of communities with mixed hard and soft coral taxa and functional traits (McClanahan, Darling, et al., 2020; McClanahan, Maina, et al., 2020; Reverter et al., 2022). The disconnect between the grim expectations of excess heat theory and observed persistence of coral cover in excess heat-affected locations could eventually undermine confidence in International Panel for Climate Change predictions (Hoegh-Guldberg, Jacob, et al., 2018). High spatial variability and poor correspondence in predictions of the various metrics and modeling approaches in predicting the impacts of climate change on coral reef communities highlight the need for more empirical tests of efficacy.

Regardless of the specific metric or study, most current locations published in the literature can be classified as avoidance refugia. Categorizing the locations of refugia identified from the literature into 3 types indicated that 97% of the 35 refugia publications evaluated used at least 1 avoidance metric (Appendix S1). When studies were classified based on the 7 combinations of the 3 refugia options, 51% of all studies used avoidance metrics only. This increased to 63% for studies in which only thresholds metrics were used. The remaining studies were classified as avoidance combined either with resistance (17.1%) or with recovery (11.4%) (Figure 1b). One Brazilian study used resistance metrics alone (Mies et al., 2020), and none used recovery metrics alone or resistance and recovery combined, despite the early suggestions of West and Salm (2003). Variability models generally distributed their metric more evenly; 26.3% used all 3 types of metrics, whereas among threshold model studies, only 6.3% used all 3.

Resistant corals and locations may be particularly underrepresented if the current avoidance-dominant metrics remain highly reliant on a few related excess heat variables. An unequal distribution of key metrics poses a problem for conservation prioritization and building a balanced set of climate refugia. For example, what if low excess heat or avoidance refugia are eventually destroyed as thermal heat waves increase in duration and extent (Skirving et al., 2019)? Therefore, it makes sense to distribute conservation efforts and risk more evenly to include more resistant and rapidly recovering locations.

Identification of coral refuges is based solely on a few highly correlated measures of excess heat and related factors. Therefore, there is a high risk that the conservation focus will only be on avoidance refuges that allow corals to avoid the impacts of climate change, rather than refugia where coral reefs can adapt to the impacts of climate change. Future proposed locations need to be evaluated for their abilities to avoid (exposure), resist (sensitivity), and recover. Identifying coral reef refugia to climate change can be improved by recognizing coral sensitivity and recovery, such as adaptive capacity, that reduces sensitivity to exposures (Bairos-Novak et al., 2021). Adaptive capacity is increasingly being recognized as highly variable among taxa and locations and influenced by connectivity (Asner et al., 2022; Eladawy et al., 2022; McLachlan et al., 2020; McManus et al., 2021). Sensitivity to thermal exposure is variable at many spatial scales and likely driven by interactions between historical exposure and species acclimation and adaptation (Louis et al., 2016; Evensen et al., 2022; McClanahan, Darling, et al., 2020; McClanahan, Maina, et al., 2020). Although this variability is acknowledged, it is seldom understood well enough to be explicitly modeled when making predictions. For example, there are cases of negative and positive adaptive covariation with stresses. These do not always reflect hard trade-offs that could hinder adaptation to thermal stress and other stressful factors, such as acidification or low dissolved oxygen (Wright et al., 2019; Alderdice et al., 2021). Regardless, refugia model predictions need testing with empirical field data and evolutionary models if they are to predict intended outcomes, such as coral cover, diversity, and reef calcification functions. Many questions need answers if current refugia policies, planning, and applications are to improve.

FINDING SOLUTIONS

A portfolio of climate refuges can still be created for the future, even with limited information. For example, we evaluated the spatial predictions of coral refugia from 15 studies published from 2003 to 2021 (details in Appendix S2). We classified each study as a threshold model or variability model from an evaluation of the variables used in the modeling analyses (Figure 3). Compiling and mapping refugia illustrated the potential for identifying coral reef locations and a portfolio of climate refugia that is not overly reliant on excess heat thresholds and avoidance criteria (Figure 4). The observed spatial mismatch of locations based on the methods was expected because models and predictor variables were often different. Nevertheless, differences in models provide an opportunity to identify spatially overlapping predictions and to compare the strength of alternatives.

Our results suggest that avoidance refugia are only a subset of a much larger set of potential refugia. Moreover, additional criteria, such as ecological and governance information, will further affect selections and the diversity of refugia. Global data sets of coral reef field observations, such as coral cover and community composition, are critically needed to improve the spatial resolution of refugia models and predictions. To make the current portfolio of climate refuges more comprehensive, one can add refuges that focus on the resistance and recovery of corals, in addition to those identified based on their ability to avoid excess heat. The high potential coverage of refugia mapped in the 15 studies produced either a hopeful view of the future or one that suggests a need to critically evaluate current selections to strengthen the strategic portfolio. Given the poor and declining ecological state of coral reefs globally, there is a clear need to improve the predictive ability of metrics and model approaches.

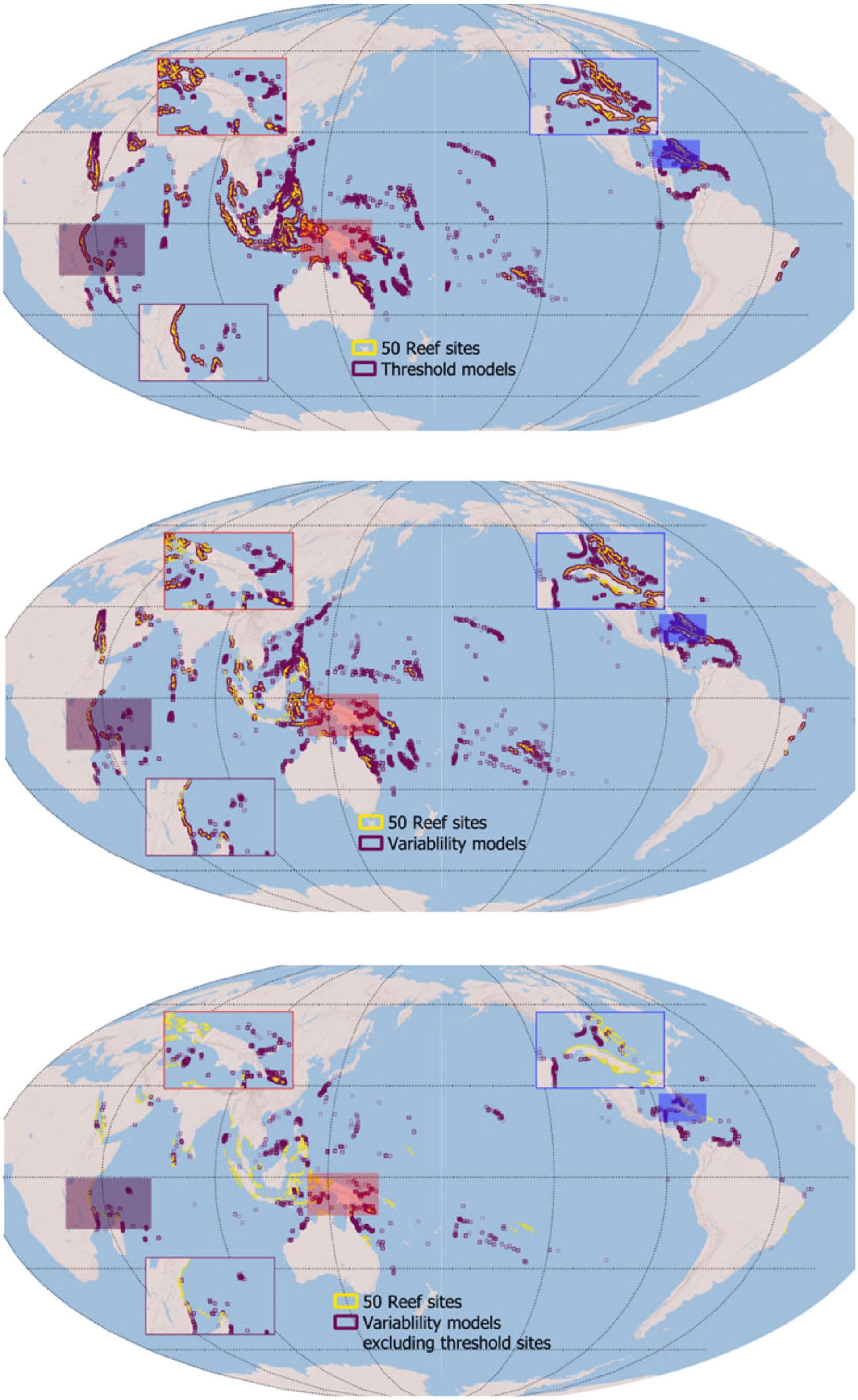

FIGURE 4 Locations of substantial climate refugia identified in 14 published studies of climate refugia for coral reefs (yellow, locations identified by threshold methods of Beyer et al. [2018] known as 50 Reefs; top panel purple, locations from 9 studies in which threshold metrics and low thermal stress were used as selection criteria; middle panel purple, locations from 5 studies in which environmental variability methods were used; bottom panel purple, 14 models showing unique variability locations identified by variability models after exclusion of threshold locations). Studies included in each panel are more fully described in Appendix S2.

To develop a more representative global portfolio of refugia with avoidance, resistance, and recovery characteristics, we make the following suggestions for conservation science and practice (Table 2).

First, a better understanding of the dynamics of coral resistance and recovery refugia to climate change at local scales is needed. For example, after prolonged exposure to heat stress, what are the characteristics of coral reefs that can resist and recover? Detailed field observations of coral communities over bleaching events that can distinguish the least stressed, most resistant, or fastest recovering corals at smaller scales will be critical to developing metrics and proxies at larger areas relevant to conservation, including national, regional, and global scales. Given that ecoregional differences in coral sensitivity can be shaped by local ecological and evolutionary histories, identifying local characteristics of resistance and refugia may scale up to larger conservation priorities and a global portfolio of refugia (Eladawy et al., 2022; McClanahan, Maina, et al., 2020). By using more environmental metrics and proxies from satellites, one can gain a better understanding of the relationships between the environment and biodiversity at larger spatial scales (Pilowsky et al., 2022). Augmenting satellite-based metrics with artificial intelligence and detailed local field studies that include coral taxa and life-history dynamics should further improve predictions of climate refugia for coral reefs (van Woesik et al., 2012; Darling et al., 2019; Santana et al., 2023).

Second, more representation of resistance and recovery refugia needs to be included in global portfolios of climate change refugia. For example, global conservation strategies for coral reefs, such as 50 Reefs, currently overemphasize avoidance refugia. Extending this portfolio to include locations with a mix of high coral cover, diversity, and adaptive potential in high-exposure locations can include resistance and recovery locations in the next iteration of a global coral reef conservation strategy. This will require commitment to and funding of collaborative coral reef monitoring efforts to compile robust, standardized, and comparable empirical data sets of coral communities and their change over time and modern statistical evaluations, such as machine learning algorithms, that can account for the diversity of environmental variables available from remotely sensed satellite data (McClanahan & Azali, 2021; Santana et al., 2023; Vercammen et al., 2019). Moreover, including coral taxa and life-history resolution in environmental niche models may also provide insights into the locations of resistance and recovery refugia for coral reefs (Cacciapaglia & van Woesik, 2015, 2016).

BUILDING A STRONGER REFUGIA PORTFOLIO

We suggest several options for improving predictions of coral reef avoidance, resistance, and recovery refugia to climate change. First, a variety of models based on field data need to be compared. Predictions should be improved by undertaking more tests of fit between environmental models and globally comparable field survey data sets of coral cover and community composition. Models should prioritize outcomes that coral reef stakeholders find most relevant; these include coastal protection, fisheries production, and biodiversity. Yet, most studies have evaluated coral bleaching, coral mortality, and coral cover, and fewer have examined coral life histories, biodiversity, and ecosystem functioning that relate to the outcomes most relevant to policy and management (Darling et al., 2019; Perry et al., 2018). Variables and models need to be demoted and promoted more rapidly through the standard competitive scientific process. Some poor models and variables persist despite low predictive skill, which could be rectified by greater adoption of variable selection and machine learning options. Artificial intelligence algorithms can facilitate the increasingly large amounts of collectively shared satellite and field data.

An outstanding question is whether excess heat predictions and bleaching are the most useful variables to evaluate reefs. Could coral mortality, recruitment, community structure, numbers of taxa, and reef fish diversity or productivity be of equal or greater concern? Slower responding variables, such as coral cover, growth, vertical relief, suitable substrate, recovery rates, or some aspect of the coral community, might be better proxies for policies and management that safeguard ecosystem services in a future of climate-driven loss and damage. Furthermore, scientists should prioritize modeling efforts that directly address the above critical ecosystem services.

The number of environmental metrics and proxies at modest scales, often <10 km^2, has proliferated in recent times (Tyberghein et al., 2012; Yeager et al., 2017). This makes it increasingly possible to make proxies and predictions for many benthic and coral metrics (Li & Asner, 2023) if there are globally standardized and comparable data sets of field information freely available, including those aligned with the principles of open science. For example, satellite data, machine learning algorithms, and coral cover compilations have uncovered key environmental variables considerably different from excess heat (McClanahan & Azali, 2021; Santana et al., 2023; Vercammen et al., 2019). Niche models are another example. Future niche models will need to include the variables that best determine coral distributions, which is not likely to be the current default of mean ocean conditions (Lee-Yaw et al., 2021). Therefore, there is a need to include aspects of chronic and acute temperature variabilities, light, calcium carbonate concentration, dissolved oxygen, turbidity, currents, and connectivity (McClanahan, 2020). Inclusion of chronic and acute stress derived from a variety of environmental metrics should help build better models and improve conservation.

A well-known statistical observation is that models based on the past are often poor predictors of the future. This repeated finding evokes problems when evaluating and comparing models. For example, a variability model (Maina et al., 2011) was good at predicting coral cover immediately after the 1998 bleaching event but was less effective thereafter, possibly because of acclimation and community change (McClanahan & Azali, 2021; McClanahan et al., 2015; McClanahan, Maina, et al., 2020). Consequently, an avoidance model parameterized after the 1998 bleaching event would be expected to lose predictive ability as the "relentless march of mass coral bleaching" proceeds (Skirving et al., 2019). The proposed change from

TABLE 1 Locations recommended in the literature as coral reef refugia.[a]

Location[b]	Description	Refugia type	Refugia criteria	Supportive studies	Nonrefugia criteria	Nonsupportive studies
Indian Ocean						
Northern Mozambique	Deep-water channels of Nacala and Pemba and Quirimbas Island may be providing local thermal refuge	Avoidance, high diversity	Low thermal stress; high biodiversity and persistence over time	McClanahan & Muthiga, 2016; McClanahan et al., 2007, 2011	Weak management of Quirimbas protected areas and destructive fishing common	Gill et al., 2017
Northern and Eastern Madagascar and Mayotte	Stable temperatures but patchy distribution of coral reefs	Avoidance, high diversity	Low thermal stress and high biodiversity and persistence	Heron et al., 2016; McClanahan & Azali, 2021; McClanahan et al., 2009, 2011;	Cyclones common and can be damaging depending on exposure	Puotinen et al., 2020
Southwest and west Madagascar (Toliara reef complex)	Documented return to coral assemblage dominated by *Acropora* and other branching taxa after 2015–2016 bleaching event	Avoidance and recovery	Low thermal stress and high recovery; high biodiversity; persistence of sensitive taxa	Botosoamananto et al., 2021; Cacciapaglia & van Woesik, 2015	High temperature skewness; degraded reefs with poor fisheries; watershed management	Bruggemann et al., 2012; Maina et al., 2012; McClanahan et al., 2009, 2011; van Hooidonk et al., 2016
Southeast Mauritius	Repeated thermal disturbances caused declines in all taxa except for *Acropora* in nearshore environments	Recovery	Low thermal stress and internal tidal buffering; fast recovery of *Acropora* after mass mortality	Maina et al., 2008; McClanahan & Muthiga, 2021; Storlazzi et al., 2020	Loss of many non-*Acropora* taxa	McClanahan & Muthiga, 2021
Northwest Mauritius	Species lost in southeast persisted in the northwest of the island	Resistance	Low thermal stress and internal tidal buffering; persistence of stress resistant taxa after mass mortality	Maina et al., 2008; McClanahan & Muthiga, 2021	Loss of thermally sensitive taxa	McClanahan & Muthiga, 2021

(Continues)

TABLE 1 (Continued)

Location[b]	Description	Refugia type	Refugia criteria	Supportive studies	Nonrefugia criteria	Nonsupportive studies
India—southeast India, Gulf of Mannar	Persistence of coral cover following successive bleaching events	Resistance, recovery	Stress-tolerant species increased in relative abundance after bleaching events in 1998, 2010, and 2016; potential acclimation to mild bleaching almost every summer; western reefs in Gulf of Mannar show signs of being an important refugia	Raj et al., 2021		
Southern India, Maldives, Chagos Islands, Seychelles	Long island chains may have considerable variability that may provide some refuge	Avoidance, recovery	low excess thermal stress; future increase in habitable niche area; high reef density; low number of cyclones	Cacciapaglia & van Woesik, 2016; Heron et al., 2016	High total thermal exposure; frequent passing of thresholds; low coral tolerance; low acclimation potential; poor coral status	Maina et al., 2011; McClanahan & Azali, 2021; McClanahan et al., 2020; Teneva et al., 2012
Western Australia reefs include islands of Montebello, Ningaloo, Shark Bay, and Houtman Abrolhos	Multiple environmental and coral community variables used to make predictions of persistence	Avoidance, resistance	High future habitable area; persistence of taxa and low thermal and cyclonic stresses; high resistance	Cacciapaglia & van Woesik, 2015; Zinke et al., 2018	High excess thermal stress; cyclones in north	Beyer et al., 2018
South Africa	Low thermal stress; hard coral diversity low and replaced by soft corals	Avoidance	Low thermal stress; internal tidal waves; low bleaching and persistence of taxa	Maina et al., 2008; Reigl & Piller, 2003; Storlazzi et al., 2020	Low to modest hard coral; high soft coral diversity	Schleyer & Porter, 2018
Northern Red Sea	Indication of low stress and high tolerance to stress	Avoidance, resistance	Low total thermal exposure; reduced light penetration; low coral sensitivity	Cacciapaglia & van Woesik, 2016; Osman et al., 2018	High periodic thermal stress	van Hooidonk et al., 2013
Western Pacific						

(Continues)

TABLE 1 (Continued)

Location[b]	Description	Refugia type	Refugia criteria	Supportive studies	Nonrefugia criteria	Nonsupportive studies
Equatorial Pacific (Micronesia, northern Marshall Islands, Solomon Islands, Vanuatu, French Polynesia, Fiji, Carolinian ecoregion)	Persistence of low thermal stress niches and high cloud cover; low sensitivity to thermal fluctuations that suggest tolerance to repeated stress; recovery with heat-tolerant symbionts and low human disturbance	Avoidance, resistance, recovery	Niche modeling; low sensitivity; high cloud cover; recovery with heat-tolerant symbionts and low human disturbance	Cacciapaglia & van Woesik, 2015; Claar et al., 2020; Gonzalez-Espinosa & Donner, 2021; Hoegh-Guldberg, 1999; Maina et al., 2011; McClanahan et al., 2020; Mollica et al., 2019; van Hooidonk et al., 2013	High sea surface temperature and rate of rise; low aragonite saturation; equatorial areas with frequent repeats of excess thermal stress	Beyer et al., 2018; Donner et al., 2005; Guinotte et al., 2003; van Hooidonk et al., 2013
Western and northern Philippines, Palawan	Persistence of low thermal stress	Avoidance	Low thermal stress	McLeod et al., 2010; McManus et al., 2020		
Northern Borneo, Solomon Sea, eastern Papua New Guinea	Low bleaching; persistence of corals reported	Avoidance, resistance	Low thermal stress	McLeod et al., 2010; McManus et al., 2020	High DHW and SST rate of rise	McLeod et al., 2010; van Hooidonk et al., 2013
Southern Great Barrier Reef	Low thermal stress; low sensitivity of corals	Avoidance	Low thermal stress	Hock et al., 2017; Kim et al., 2019; MacNeil et al., 2019; van Hooidonk et al., 2013		
Thailand, Vietnam	Low excess thermal stress; niche availability	Avoidance	Low excess thermal stress; low resistance	Cacciapaglia & van Woesik, 2016; van Hooidonk et al., 2013	Rapid temperature rises; low and patch resistance to thermal stress	Hoegh-Guldberg, 1999; McClanahan et al., 2020
Northern Japan	Low thermal stress; high turbidity; high internal waves; high recovery	Avoidance, recovery	Low thermal stress; high recovery; low resistance	Cacciapaglia & van Woesik, 2015; Storlazzi et al., 2020	Low resistance to thermal stress	McClanahan et al., 2020
Hawaii	Low thermal stress; persistence across thermal stress events in some locations	Avoidance	Low thermal stress	Ritson-Williams & Gates, 2020		
New Caledonia	Variable stress; recovery potential	Avoidance, recovery	Low thermal stress; recovery potential	Selmoni et al., 2020	Variable locations based on island aspects	Selmoni et al., 2020
Eastern Pacific	Patchy upwelling and bleaching suggest some local refuge	Avoidance, recovery	Sea surface temperature and aragonite saturation and rate of rise; upwelling	Guinotte et al., 2003	High bleaching and mortality; low diversity; many reefs have been lost	Glynn et al., 2018
Caribbean/Atlantic						

(Continues)

TABLE 1 (Continued)

Location[b]	Description	Refugia type	Refugia criteria	Supportive studies	Nonrefugia criteria	Nonsupportive studies
South Atlantic, Brazil, Abrolhos Bank	Low thermal stress; high turbidity; persistence of coral over time		Low thermal stress; tolerance of corals	Mies et al., 2020	Low diversity; unusual taxa	Mies et al., 2020
Bermuda, Bahamas	Temperature location results in low thermal stress	Avoidance	Low excess heat thermal stress trends	Muñiz-Castillo et al., 2019; Riegl & Piller, 2003; van Hooidonk et al., 2016; Welle et al., 2017	Bahamas locations patchy in terms of exposures	Muñiz-Castillo et al., 2019; van Hooidonk et al., 2016; Welle et al., 2017
Belize	Persistence of *Acropora* since 1900s on local reefs; hotspots of structural complexity in Mesoamerican reef system	Resistance, recovery	Despite storms and bleaching, *Acropora* persist (possibly due to distance from the impacts of riverine terrestrial influx)	Greer et al., 2020; Randazzo-Eisemann et al., 2021	In Gulf of Honduras, frequent hurricanes, watershed runoff, and fishing stresses	Kjerfve et al., 2021
Belize, Guatemala	High coral cover; recovery after bleaching; persistence of *A. palmata*; no hurricanes	Resistance, recovery	recently discovered channel reef complex, Cayman crown; proximity to 300-m depth and freshwater lens from nearby river; very high coral cover (>75%); large healthy colonies maintained despite bleaching in 2019	Proximity to cooler waters; unique oceanography; high recovery and coral cover		Kjerfve et al., 2021

(Continues)

TABLE 1 (Continued)

Location[b]	Description	Refugia type	Refugia criteria	Supportive studies	Nonrefugia criteria	Nonsupportive studies
Northern Gulf of Mexico (Flower Gardens)	Low thermal stress; high currents; low light; high turbidity; persistence of coral over time	Avoidance	Low thermal stress; upwelling	Cacciapaglia & van Woesik, 2016; Chollett & Mumby, 2013; Welle et al., 2017	High cumulative and rate of change in southern Gulf of Mexico	Muñiz-Castillo et al., 2019
Northeastern Yucatan, Mesoamerica	Low cumulative thermal exposure and rate of change	Avoidance	Low thermal stress and human impact	Chollett & Mumby, 2013; Randazzo-Eisemann et al., 2001	High excess heart; patch loses of sensitive taxa; high algal cover; excess heat increases to the south	Beyer et al., 2018; Heron et al., 2016; Muñiz-Castillo et al., 2019
Eastern Colombia, Southern Caribbean Antilles, Bonaire	Low thermal stress; high cloud cover	Avoidance	Low thermal stress	Chollett & Mumby, 2013; Donner et al., 2005; Gonzalez-Espinosa & Donner, 2021; Guinotte et al., 2003; Randazzo-Eisemann et al., 2001; Welle et al., 2017	May be considerable variability in terms of exposure and responses to currents	Welle et al., 2017
Bay of Cartagena, Colombia	One of best coral reefs in Caribbean; up to 80% coral cover; dominated by *Orbicella* spp. coral colonies >3 m in diameter; scleractinian richness of at least 30 species	Resistance	Persist despite high turbidity, high thermal stress, and repeated human disturbances	López-Victoria et al., 2015; Pizarro et al., 2017		

[a] Full citations are in Appendices S1 and S2.

[b] Selected to minimize contradictions in the literature, such as when studies disagree about vulnerability or refugia status.

TABLE 2 Specific recommendations for expanding the process of identifying coral refugia.

Recommendations to improve modeling	Recommendations for users of model outputs
Diversify theory, types, and numbers of methods and variables examined for the identification of refugia.	Keep avoidance refugia as a core part of the refugia portfolio but reconsider exposure variables most important for promoting avoidance.
Evaluate and include interactive roles of acute and chronic stress for making better predictions of response variables, such as cover, diversity, and functions.	Engage locally knowledgeable people to ensure proposed refugia are supported by their local knowledge.
Embrace regional and local assessments of reef status and fine-scale modeling to take advantage of local conditions and knowledge to help identify refugia at fine scales.	Work toward a balanced set of environmental and ecological criteria for site selection that balances inclusion and combinations of avoidance, resistance, and recovery refugia.
Improve predictions and protection of key services rather than just coral responses to excess thermal exposure, including calcification, biodiversity, and fisheries production.	Better define and continuously readdress selection and mapping of refugia as lessons are learned from successes and failures.
Engage the climate modeling community to include variables that affect corals to improve their predictions of their status in global models.	Build capacity of local reef practitioners to identify and monitor coral reef refugia.
Embrace uncertainty and skepticism by continuously testing models for failure and using them as opportunities for learning.	Include political support and feasibility of management when making refugia investment decisions.
Build and test models for future predictions, given that models relying on past thermal responses may have limited predictive ability.	Evaluate governance context and build capacity to overcome limits to human engagement in solutions.

avoidance to resistance and recovery refugia may not necessarily improve the predictions of specific models, but the process should reduce risk and avoid failures by creating a broader portfolio of models and refugia types that can be actively evaluated to ensure diverse attributes and outcomes (Webster et al., 2017).

Another option is to create ensemble models of refugia prediction. Combining models will better address future uncertainty and thereby prioritize locations based on multiple models, an approach that is often used in climate modeling to improve predictions of future states. For example, when several models predict the same refugia location, these are no-regrets locations that can inform policies that establish conservation investment priorities. The process of variable and model selection inclusion does, however, need to pass some thresholds of predictive power. That is, from the above models, some will fail to meet minimum criteria or be uncompetitive relative to other models. Weakly predictive variables and models can eventually be dropped to strengthen a growing refugia prioritization portfolio.

To create a strong and comprehensive conservation portfolio, models based on different assumptions, variable choices, and weights need to be developed. This may seem like an onerous task; however, the ensemble model approach used by global climate modelers has helped avoid overreliance on specific, overfit, and weak predictions that can arise from using highly correlated variables. Furthermore, including the increasingly available biogeographic, oceanographic, and other environmental variables outside the usual DHW metrics is expected to improve future refugia models (Pilowsky et al., 2022). For example, coral thermal optima and mechanistic coral ecoevolutionary models have made coral cover predictions over time (Logan et al., 2021; Matz et al., 2020; McManus et al., 2021). These mechanistic models can be compared with observed ecological conditions and statistical or empirical fit models. Although mechanistic models can lead to more robust predictions than statistical models under novel environmental conditions (Cuddington et al., 2013), there are considerable uncertainties surrounding the mechanisms and the genetic diversity of different species, gene flow patterns, connectivity, and genetic architecture of stress tolerance, among other blind spots that can produce surprises. As conditions for coral survival and biodiversity change rapidly, grounding scientific models in observed field data will be crucial.

Comparing fundamentally different models and finding spatial overlap in refugia is possible. Specifically, predictions of coral cover from a variability model and a threshold model were compared with 2050 predictions of coral cover from the Coupled Model Intercomparison Project (CMIP) (Cornwall et al., 2021; McClanahan & Azali, 2021). The variability model used 7 variables derived from fits to coral cover field data, whereas the threshold model used the common excess heat variable. Threshold variables were considerably weaker than the 6 continuous variables used in the variability model. Nevertheless, refugia of sites with coral cover >25% in 2050 were predicted by both models, but the variability model predicted a far larger number and geographic spread of refugia than the threshold model. Yet, there was sufficient overlap to suggest an area of no regrets from northwest Madagascar to the African coastline from southern Kenya to northern Mozambique, an area known for its high biodiversity that may indicate a refuge on a geologic scale (McClanahan et al., 2011). Spatial resolution of models and overlapping locations is a perennial concern, but new globally consistent tools can reduce bias (Lyons et al., 2020). Consequently, these ongoing efforts suggest ways to expand the reef conservation portfolio to avoid blind spots, bias, and overreliance on a few metrics and options.

Statistical models require openly and freely available field data, which are scarce, but field compilations are increasing and now sufficient for many scales, even globally (Darling et al., 2019; van Woesik & Kratochwill, 2022; https://datamermaid.org/). Spatial and temporal scales of resolution and data quality are frequent concerns and caveats of all published modeling papers. However, less frequently mentioned limitations are the above types of foundational model structures, variable choices, and ensemble model approaches. Scale resolution should not matter when the model structure and choice of variables are weak. Science promotes generality, global views, and associated publications, but management and refugia identification may benefit more from the use of local data and implementation at finer scales.

BUILDING AN OPEN-SCIENCE PLATFORM

A fundamental concern for all reef stakeholders is improved understanding of the effects of climate change on coral reef growth, coastline protection, fisheries production, and other reef services (Perry et al., 2020; Reverter et al., 2022). Yet, decisions have been and will continue to be made in the absence of critical knowledge. We outline a collaborative approach to provide a more comprehensive understanding of the consequences of climate change for coral reefs and future ecosystem services that should promote a more diversified and learning-based approach to refugia.

Large data sets need to be made available to modelers working at various scales. There are several efforts to collect reef data from field observations and remotely sensed satellite observations at large scales, including the Global Coral Reef Monitoring Network, Reef Check, MERMAID, Reef Life Survey, ReefCloud, and the Allen Coral Atlas. Continued efforts to ensure standardization of field methods and data models are critical, including interoperability among different databases. Efforts to analyze and model these data often depend on the specific interests and potential biases of investigators and funders. This is not enough to ensure global, open-access, robust field data sets and requires substantial reprioritization by scientists, monitoring initiatives, funders, and policy makers. Additionally, coral stress responses are often evaluated rather than ecosystem services, which are more likely to provoke societal support for better management of coral refugia. Finally, many new and important variables that could provide better connections to human needs have been recognized, but many are not being modeled. Initiatives, such as Earth System Models and CMIPs, should seek advice from coral reef ecologists and social scientists to identify variables that predict ecosystem services at appropriate scales for transformative policies. In some cases, this may require scaling down from global mapping to national or regional scales of conservation and resource management, such as fisheries and watershed management. Specifically, variables needed at finer scales for future projections include SST variability, calcium carbonate concentrations, dissolved oxygen, turbidity, and nutrients.

Often critical but overlooked is the governance context and the ability and willingness of stakeholders to effectively engage in solutions. No amount of science can overcome a social inertia that prevents action or limits actions to short-term interests. 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 (Hampton-Smith et al., 2021; McClanahan et al., 2006, 2015). Short-term production of food or wealth, 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 weak histories of supporting conservation without external support (McClanahan & Rankin, 2016). Governance policies that subsidize extraction rather than the protection of natural resources are likely to increase human and natural resource poverty (Sumaila et al., 2016). Future efforts may be better served by considering enabling conditions, such as political will, feasibility, and the cost and benefits of management based on historical success (Jones et al., 2018). There are locations in tropical nations with histories of effective reef conservation that can form a basis for evaluating the principles of success (Cinner et al., 2016).

Any effort to improve predictions is going to require the principles of continuous risk assessment and learning. That is, exploratory and adaptive science are 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 programs. Future scientific efforts for reef conservation need to encourage and support diverse approaches and avoid the pitfall of seductive or monolithic theories. At the same time, managers must be prepared to learn and adapt as global and local stressors produce 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 reef conservation. Furthermore, future conservation efforts must include continual trialing and updating of information, combinations of empirical surveys and environmental remote sensing information, and close work with managers, stakeholders, scientists, and funders to develop critical conservation priorities for coral reefs from local to regional to global scales.

CONCLUSIONS AND RECOMMENDATIONS

Based on our review of 30 years of climate refugia studies, many locations could be classified as potential refugia for coral reefs and priorities for conservation (Table 1; Figure 4; Appendix S1). However, portfolios of climate refugia must be based on empirical field-based examinations of relationships among key metrics of coral cover, diversity, and ecosystem services; for example, connecting climate forecasting to empirical compilations of field data to show where the highest coral cover and biodiversity is or is predicted to occur. A specific example of identifying refugia described above is the mapping of the distribution of excess heat globally and its hump-shaped relationship with coral cover. This relationship indicates peak coral cover at intermediate excess heat. Knowing where these peak locations occur can help identify where potentially high coral cover, biodiverse, and functioning reefs occur at a global scale. Additionally, given the global diversity, coverage, and accessibility of ocean variables, it is now feasible to create more sophisticated multivariate models to improve the future climate refugia portfolios; specifically, by combining observations of coral communities and remotely sensed environmental variables with artificial intelligence and machine learning. It is now possible to create more accurate predictive ensemble models, similar to those used to make climate predictions provided by the CMIP.

There are several scientific needs to improve identification of coral reef refugia (Table 2). First, variables predictive of avoidance, resistance, and recovery refugia need to be identified and evaluated to improve conservation of coral reefs. This process of scientific discovery and policy implementation will provide important learning by reducing current blind spots and increasing adaptive management of coral reefs and the ecosystem services they provide to nearly 1 billion people. Beyond global efforts to identify better methods and refugia, there is a need to increase support for local and regional downscaled refugia portfolios and to match the scale of scientific studies to the scale of governance and policy actions and include social, economic, social governance, and political will when designing global portfolios of conservation action. Coral reef scientists from broad disciplines need to be engaged in these initiatives to ensure their decisions are based on the best evidence. The success of such efforts depends on improving large-scale and freely available data-driven monitoring of coral reef biodiversity and ecosystem functioning. This will ensure that science and policy action have the best information with which to identify climate refugia and catalyze global action to secure the future of coral reefs in a changing climate.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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