Coral conservation requires ecological climate-change vulnerability assessments

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Climate-driven changes to environmental conditions are driving severe declines of coral reef ecosystems. Current climate vulnerability estimates commonly focus on ocean warming and typically overlook ecological responses or use broad proxies to represent responses, leading to management decisions based on incomplete views of coral reef futures. We explore four underdeveloped aspects of climate vulnerability assessments and make the following recommendations: (1) use climate projections based on changes in global warming as future scenarios in place of the more common emissions scenarios; (2) include available high-resolution projections for climate variables in addition to thermal stress; (3) combine projected climate stressors accounting for uncertainty in future outcomes; and (4) quantitatively assess historical and project future ecological sensitivity and adaptive capacity of corals to multiple stressors. We demonstrate how this framework can be used to reduce uncertainty in projected climate vulnerability and facilitate targeted investment in managing reefs most likely to endure climatic disturbances.

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Climate-change impacts on tropical marine ecosystems are extensive and increasing in severity as global greenhouse-gas (GHG) emissions continue to rise (Hughes *et al.* 2018). The decline of coral reef systems worldwide is of extreme concern due to the considerable economic and ecological value associated with the planet's most biodiverse marine ecosystem (Hughes *et al.* 2017a). Coral reef climate vulnerability refers to the predisposition of coral species, populations, and/or communities to be negatively affected by climate change, and encompasses three aspects: climate exposure, ecological sensitivity, and adaptive capacity (Dawson *et al.* 2011). Current management solutions generally focus on removing local threats from reefs that are least vulnerable to climate change (Beyer *et al.* 2018), and therefore global policy and regional or local reef management depend on robust estimates of spatiotemporal climate-change impacts on marine habitats. However, the diverse range of factors affecting ecological responses to multiple climatic changes complicates coral reef vulnerability assessment (Safaie *et al.* 2018), leading to uncertain or incorrect estimates that potentially compromise climate-change-resilient management strategies.

In a nutshell:

- Coral reef management under climate change is hindered by the inability to evaluate differences in reef vulnerability
- Using changes in global mean temperature (eg 1.5°C or 2.0°C) instead of emissions pathways can reduce uncertainty in future warming scenarios
- Stressors other than thermal stress should be included in vulnerability assessments; high-resolution climate projections are available for other coral reef-relevant climate variables
- Interactions among stressors can be applied to projected climate stressors by utilizing statistical techniques that account for uncertainty in future scenarios
- Past ecological responses to multiple climate disturbances must be used to project responses to future climate conditions to estimate ecological climate vulnerability

Climate-relevant conservation for coral reefs requires global climate-change mitigation along with the establishment of marine protected areas that control local-scale threats and consequently reduce the combined impact of global-scale stressors (Tittensor *et al.* 2019). The dismal outlook for the future of coral reefs has forced conservation efforts into two general approaches: protect the least exposed areas (Beyer *et al.* 2018) or protect a range of areas subjected to varying exposure regimes (Webster *et al.* 2017). Identifying a range of areas minimizes uncertainty associated with ecological responses to historical warming and bleaching events (Mumby *et al.* 2011), and incorporates multiple habitat types subjected to varying levels of exploitation (Webster *et al.* 2017). However, climate conditions are projected to render large areas uninhabitable to corals, and – in light of limited conservation resources – protecting low climate exposure areas will be considered most efficient because they are more likely to survive (Beyer *et al.* 2018; Mcleod *et al.* 2019). This selective identification of the least-exposed sites can be successful only if exposure estimates prove to be correct (Webster *et al.* 2017) and if exposure is a valid predictor of reef vulnerability.

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Challenges in coral reef climate vulnerability assessments

Coral reefs are impacted by a range of global-scale environmental changes, of which past and future ocean warming are most commonly used to evaluate the risk of reefs experiencing large-scale coral bleaching and mortality, typically using cumulative thermal stress metrics like degree heating weeks (DHWs) or degree heating months (DHMs). DHWs and DHMs refer to the accumulated weekly or monthly sea-surface temperature (SST) anomalies, also known as hotspots, that exceed the long-term maximum monthly mean by 1°C or more (Donner *et al.* 2005; Liu *et al.* 2006). Bleaching occurs when reef-building corals expel their symbiotic algae under thermal stress (Hughes *et al.* 2017b), but the commonly used DHW and DHM parameterizations used to represent such ecological responses to thermal stress are now known to have limited predictive value (Ainsworth *et al.* 2016; Kim *et al.* 2019; McClanahan *et al.* 2019). Subsequent prevailing warming or cooling of the water determines whether corals die or regain their symbionts. Measures of thermal stress alone are not an indicator of coral bleaching because other environmental factors (eg daily temperature patterns, light intensity, water mixing, nutrient input; Yee and Barron 2010; Ainsworth *et al.* 2016; Donovan *et al.* 2020) influence bleaching severity and consequently predictions of bleaching events. Moreover, coral species exhibit differential responses to thermal stress, leading to varying degrees of bleaching among community types (Kim *et al.* 2019). Predicting and managing reef responses to climate-change-related thermal stress therefore hinges on our ability to accurately quantify the link between multiple exposure metrics and reef-specific responses to thermal stress, particularly with respect to bleaching-associated mortality.

Climate exposure projections are required in order for relevant conservation goals to be established, but there are model and scenario uncertainties associated with such projections (Levy and Ban 2013). There is also a spatial mismatch between the scale of climate model projections (typically hundreds of kilometers) and that of local management (1–2 km for the smallest marine protected areas) (Kwiatkowski *et al.* 2014). Downscaling techniques increase the resolution of thermal stress projections indicating the spatial distribution of low exposure areas for targeted intervention. However, ocean warming represents just one of a range of climate variables that influence ecological responses to climate change; other factors, such as storms, irradiance and UV exposure, salinity, and sea-level rise, also impact coral reefs (Ban *et al.* 2014). Storm exposure is recognized as a criterion in reef conservation for climate-change prioritizations, but is based solely on historical data (Beyer *et al.* 2018). Projected storm exposure is required to prioritize areas for climate-change management that conserve multiple communities as insurance against future damage (Webster *et al.* 2017; Beyer *et al.* 2018).

Interactions between and among various stressors further complicate assessments of projected climate exposure because the negative ecological effect may be the sum (additive), less than the sum (antagonistic), or greater than the sum (synergistic) of the combined impacts (Ban *et al.* 2014), but how these relationships will play out in the future is largely unknown (Camp *et al.* 2018). Metrics of interacting climate variables alone are likely insufficient for quantifying reef vulnerability, as varying tolerance to disturbance alters ecological responses to stress (Dawson *et al.* 2011). Failure to consider differences in disturbance-related tolerance in estimates of ecological sensitivity risks focusing scarce conservation resources in areas with low exposure but high sensitivity failing to meet management objectives. Although we focus here on management of reefs with climate vulnerability in mind, effective conservation clearly also requires consideration of other management objectives, such as addressing local stressors (eg overexploitation, pollution), and of socioeconomic factors (Mcleod *et al.* 2019).

Current reef climate vulnerability assessments typically use past climate exposure or projected thermal stress metrics alone (Figure 1; see also WebTable 1). Maximizing the success of conservation approaches requires identification of reef vulnerability with improved estimates of multiple sources of climate exposure at the relevant scale and set in an ecological context (Figure 1). For this approach, we propose the following four steps: (1) reduce uncertainty in climate model projections by assessing different levels of warming (eg 1.5°C or 2.0°C) instead of emissions scenarios; (2) make use of existing downscaled climate projections for a range of climate variables to predict future climate exposure; (3) estimate combined climate exposure accounting for different types of interactions between multiple stressors; and (4) calculate reef vulnerability using both projected, local-scale, and multi-stressor climate exposure, and ecological responses to these stressors.

Minimizing uncertainty in climate model projections

General circulation models (GCMs) that predict future atmospheric and ocean states inform exposure assessments (Frieler *et al.* 2013), but there is uncertainty associated with climate model projections (Levy and Ban 2013). Model uncertainty can be reduced using a multi-model ensemble mean. The approach assumes that biases among a range of models will be reduced or canceled out, and has been validated by the improved performance of the ensemble compared to any single model when simulating present-day climate (Knutti *et al.* 2010). However, the multi-model mean dampens extreme values that can have major ecological impacts on coral reefs (eg extreme thermal stress leading to coral bleaching) and on biological systems generally (Harris *et al.* 2018). Uncertainty in future emissions trajectories is an additional source of error exacerbated in studies selecting single emissions scenarios that are already known to be an inaccurate representation of future trajectories.

International climate policy has driven studies examining biological responses to global warming of 1.5°C or 2.0°C (Hoegh-Guldberg *et al.* 2018), although only a few examples of this exist for coral reefs (Frieler *et al.* 2013; Schleussner *et al.* 2016). We recommend that coral reef climate vulnerability studies transition from the widespread use of emissions scenarios and relatively small model ensembles to the warming-based approach for climate model projections. Assessing different global-warming scenarios removes a large proportion of the uncertainty in future emissions and varying climate model sensitivities. The warming-based approach uses a large ensemble from all models and emissions scenarios to compare regional extreme events associated with a specified change in global temperature (Mitchell *et al.* 2017). Focusing on the level of global warming allows for assessment of the risk of climate change becoming dangerous to unique and threatened ecosystems like coral reefs (Hoegh-Guldberg *et al.* 2018), with results that are compatible with international climate policy established by the Paris Agreement (Mitchell *et al.* 2017).

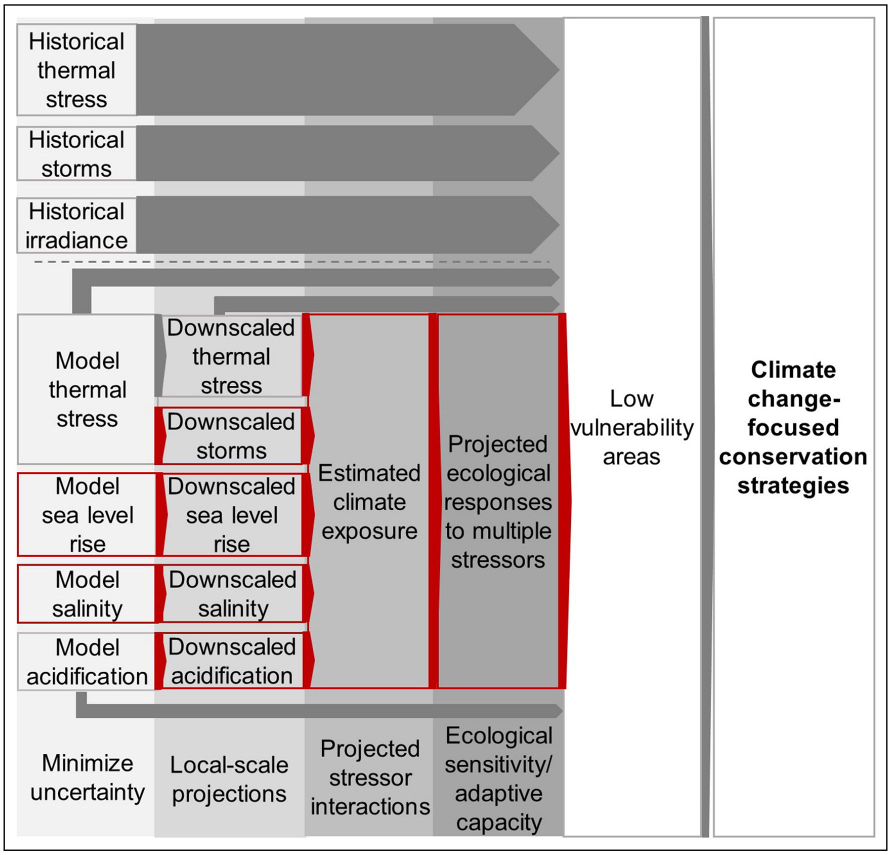

Figure 1. Schematic showing the current methods and our updated framework to assess climate vulnerability of coral reefs for conservation and climate policy. Many current approaches use historical metrics and/or climate model predictions (outlined in gray) to assess reef vulnerability, whereas fewer rely on downscaled thermal stress. Our framework is shown by the improvements outlined in red and is further detailed in the main text.

Global warming is determined by the change from a natural baseline that can be defined by a century-scale (King *et al.* 2017) or pre-industrial (Frieler *et al.* 2013; Schleussner *et al.* 2016; Mitchell *et al.* 2017) average temperature. The global warming scenarios (eg 2.0°C) are determined using all model years from all GCMs and model experiments where 10- or 20-year average temperatures are 2.0°C above the natural baseline (Schleussner *et al.* 2016; King *et al.* 2017). Available model output for each model year, such as SST, can be used to calculate extreme climatic conditions impacting coral reefs (Frieler *et al.* 2013; Schleussner *et al.* 2016). The large ensemble of thermal stress values enables robust statistical comparisons of different magnitudes of global temperature change (Schleussner *et al.* 2016), indicating the reduction in climate vulnerability that can be achieved through international climate policy. This approach reduces uncertainty in the projected climate exposure estimates that feed into climate vulnerability assessments.

Projecting climate variables to local scales

Global-scale climate models are effective in simulating historical warming at larger spatial scales, but their coarse-scale resolution fails to match the local management scales at which local processes create fine-scale variability (Kwiatkowski *et al.* 2014). Increasing the resolution of climate predictions by downscaling GCM outputs (Figure 2) improves the relevance of model projections for ecological processes and forms a better basis for identifying low exposure sites for local-scale conservation measures (Van Hooidonk *et al.* 2015). Downscaling has been applied to assess thermal stress exposure of coral reefs (eg Donner *et al.* 2005; Van Hooidonk *et al.* 2015; Wolff *et al.* 2018). Downscaled coral bleaching projections are publicly available at 4-km resolution from the US National Oceanic and Atmospheric Administration's Coral Reef Watch (Van Hooidonk *et al.* 2015), and long-term remote-sensing SST data at 1-km resolution enable the downscaling of temperature projections to even finer scales (Chin *et al.* 2017). However, downscaling has yet to be applied to other coral reef climate stressors (WebTable 1).

Although neglected in coral reef research, downscaling GCM projections of other environmental factors could improve conservation decision making (eg when applied to tropical cyclone projections). Tropical cyclones require consideration in climate exposure estimates given that the proportion of high-intensity storms is projected to increase with climate change (Knutson *et al.* 2015) and thermal stress and local-scale impacts impede coral recovery following storm damage (Puotinen *et al.* 2016). Tropical cyclones are not well simulated by global-scale climate models because they occur at relatively small spatial and temporal scales. Downscaling storms requires

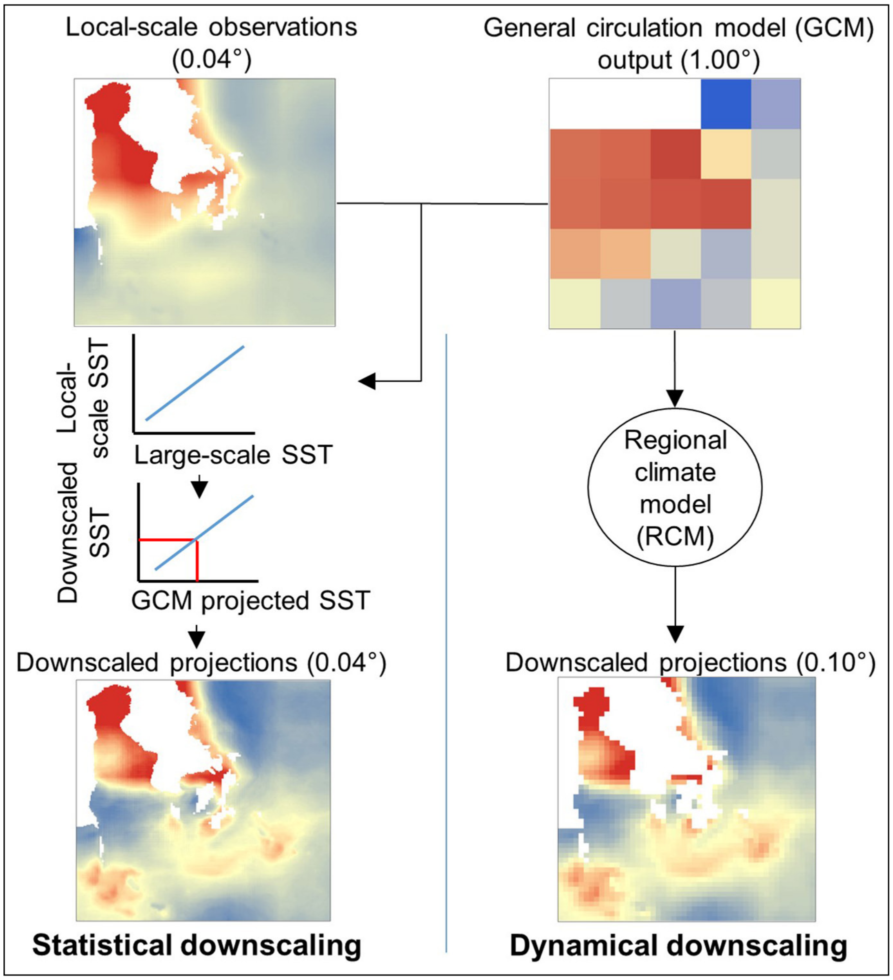

Figure 2. Summary of the main downscaling techniques. Statistical downscaling uses the relationship between the large-scale atmospheric circulation and local-scale observations (Fowler *et al.* 2007). The dynamical technique uses regional climate models with large-scale boundary conditions, such as relative temperature and humidity (Knutson *et al.* 2010). Technique selection is study specific, as each of the techniques has its pros and cons. Examples of the processes were adapted from Donner *et al.* (2005), Fowler *et al.* (2007), and Van Hooidonk *et al.* (2015). Resolutions previously used in coral reef literature are given for observed, general circulation model (GCM), and downscaled data (Van Hooidonk *et al.* 2015).

the accurate simulation of changes in storm-associated marine climate variables (eg SST) and the atmospheric processes that link these changes to storm activity (Knutson *et al.* 2015). Storms create feedbacks (eg the cooling wake associated with tropical cyclones) that further complicate the downscaling of storm projections (Carrigan and Puotinen 2014). Dynamical and statistical downscaling techniques simulate a range of tropical cyclone characteristics (Emanuel *et al.* 2008; Villarini and Vecchi 2013; Knutson *et al.* 2015) that determine coral reef damage, including intensity, size, duration, translation speed, and temporal variability (Puotinen *et al.* 2016; Wolff *et al.* 2016), as well as tropical cyclone-associated cold wakes at <10-km resolution, indicating the storm exposure distributions projected for coral reefs worldwide.

Downscaling is necessary for other abiotic factors impacting coral reefs, such as ocean acidification and light availability. These factors are also affected by local features (eg presence of carbon dioxide vents and seagrass meadows [for ocean acidification]; water turbidity and cloud cover [for light]; Camp *et al.* 2018). Dynamical downscaling is useful when the long-term records required for statistical techniques are lacking (Camp *et al.* 2018), and has been applied to other climate variables, such as salinity (Townhill *et al.* 2017), sea-level rise (Liu *et al.* 2016), waves (Wandres *et al.* 2017), and ocean acidification (Skogen *et al.* 2014; Wallhead *et al.* 2017). Although remote-sensing observational data are available for such variables as photosynthetically active radiation – a proxy for incoming solar radiation (Donner and Carilli 2019) – the dataset currently does not extend far enough back in time for establishment of a statistical relationship between the fine and large scales, and light intensity is heavily influenced by feedback processes (eg clouds) that are not captured by statistical downscaling (Van Hooidonk *et al.* 2015). However, dynamical studies are limited by their geographic extent, as they focus on small geographic areas through computationally intensive regional climate models. The next generation of GCMs involved in the High Resolution Model Intercomparison Project (HighResMIP) for the Coupled Model Intercomparison Project Phase 6 (CMIP6) provide future opportunities to incorporate higher resolution model output (eg 25-km resolution; Haarsma *et al.* 2016) for neglected climate variables in climate exposure estimates.

We recommend that currently available downscaled coral reef-relevant climate variables like tropical cyclone projections be incorporated into climate vulnerability assessments. Where regional climate models exist for coral reef regions, additional variables, such as ocean acidification and salinity, may inform regional-scale climate vulnerability assessments.

Combining projections of interacting climate stressors

Ideally, a comprehensive view of future climate exposure requires consideration of the combined impacts of interacting stressors (Hughes *et al.* 2017a). Coral reef impacts resulting from multiple stressors have been assessed extensively for the past (eg Maina *et al.* 2011; Zinke *et al.* 2018; Donner and Carilli 2019), and although projections of future interactions have been initiated (Maina *et al.* 2016; Wolff *et al.* 2018), past climate exposure for stressors for which there is greater uncertainty in projections, such as storms, is still being used (WebTable 1). Ocean warming and storms have many ecological impacts, interacting with a variety of local and climatic disturbances in a complex web of stressors that affect ecological change (Ban *et al.* 2014). Bleaching responses of corals are better predicted by the combined effects of both heat and light stress (Yee and Barron 2010), which tropical cyclones mitigate somewhat via increased cloud cover and sediment loading reducing irradiance (Ban *et al.* 2014). Storms also alleviate thermal stress by causing upwelling of cool subsurface waters, which influence coral bleaching dynamics (Carrigan and Puotinen 2014). Incidences of tropical cyclones preventing bleaching and enhancing coral recovery during thermal stress events were recorded in the Caribbean in 2005 and 2010 (Carrigan and Puotinen 2014), and eastern and western Australia in 2016 (Hughes *et al.* 2017b).

Projecting the climate exposure resulting from the two stressors must account for the uncertainty in climate projections and the strength of interactions. We introduce a novel and flexible approach that can be easily adapted for use in conservation decision making. For each reef pixel, the size of which is determined by the resolution of the climate data, the total climate exposure is dependent on the combined impacts of storm damage and thermal stress mitigated by the tropical cyclone cold wake (Figure 3). Uncertainty can be incorporated into estimates of climate exposure by combining probabilities of different exposures from large ensembles of climate models (eg using Monte Carlo simulations). We present an example of a climate exposure model incorporating both additive and antagonistic interactions between projected stressors (Figure 3). If the units of each climate exposure estimate are the same, the exposure types can be combined to inform overall risk. This example considers only physical damage by storms and thermal stress respite resulting from the cold wake, and advances the approach by Wolff *et al.* (2018) by allowing for cold wakes that are not necessarily sufficient to negate all the thermal stress for a given year (Carrigan and Puotinen 2014). Although other storm-related impacts (eg sedimentation, freshwater influx, nutrient injection; Ban *et al.* 2014) are excluded here, this serves as an example of how multiple future climate disturbances could be combined.

Combining interacting stressors for future climate projections is necessary to determine future climate exposure on coral reefs, as trends in climate variables are projected to vary in the future; for example, whereas thermal stress is projected to increase (Hoegh-Guldberg *et al.* 2018), the overall frequency of global tropical cyclones is projected to decrease (Knutson *et al.* 2020), impacting future cold wake benefits. Changes to stressor interactions under climate change may result in further climate-related impacts on coral reefs through potential feedbacks. For instance, the beneficial effect of ocean acidification on hard coral competitors like macroalgae may increase coral reef susceptibility to other stressors, such as disease, facilitating further macroalgal dominance (Ateweberhan *et al.* 2013). The type of analysis recommended here can be applied to different future scenarios to best address management objectives related to climate-change vulnerability, and should include iterative sensitivity analyses to account for uncertainty in the strengths and types of future interactions (Figure 3).

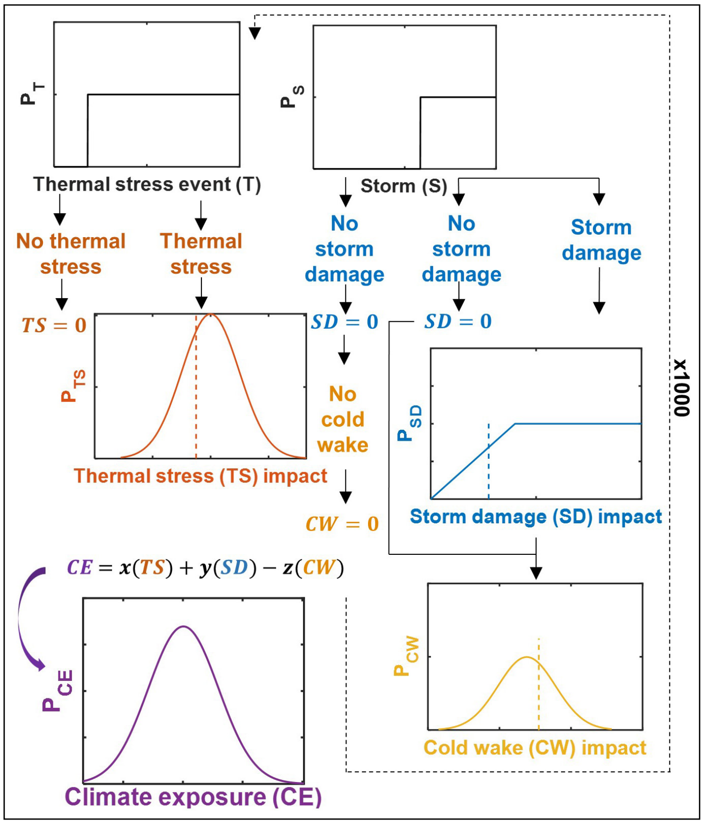

Figure 3. Probability model combining the additive and antagonistic interactions between thermal stress and storms; *x*, *y*, and *z* refer to the correlation between stressors, indicating the probability of one stressor occurring alongside another (eg a cold wake following every storm would have a correlation of 1).

Linking climate-change exposure to ecological responses and adaptive capacity

Estimates of climate exposure deriving from thermal stress projections provide an indication of the spatial variation in ocean warming, but without incorporating ecological sensitivity to environmental change, they are insufficient in determining coral reef vulnerability (Dawson *et al.* 2011). Cumulative heat stress of 4°C and 8°C weeks are commonly used to predict moderate and severe bleaching (Donner *et al.* 2005), yet these measures are now known to be inconsistent predictors of bleaching (Ainsworth *et al.* 2016; McClanahan *et al.* 2019) and do not account for variation in responses between coral species, genera, and community types (Figure 4; Kim *et al.* 2019).

Specific reef recovery responses to past thermal exposure should ideally inform any prediction of future ecological responses to projected climate exposure (Donner and Carilli 2019). However, to date, studies by Ortiz *et al.* (2014), Van Woesik *et al.* (2018), and Wolff *et al.* (2018) are unique examples of ecological responses to accumulated thermal stress (eg DHWs/DHMs) or monthly SST. These measures account for shorter term thermal extreme events causing coral bleaching and mortality, but cannot represent the

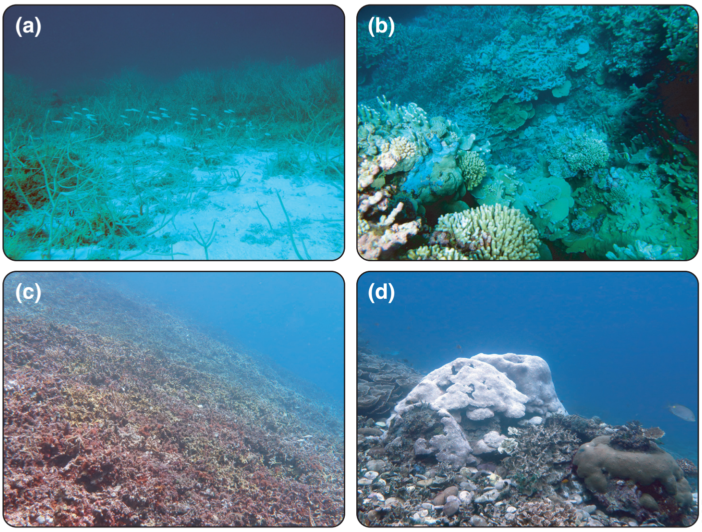

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Figure 4. Responses of coral reef communities to climate stressors are specific to community type: for example, (a) a lagoon habitat in the Marshall Islands dominated by a fine-branching coral species versus (b) a diverse reef habitat on hard substrate (also in the Marshall Islands). The habitat in (a) is sensitive to thermal stress and may experience more extensive and long-term damage following disturbance such as that depicted in (c), showing a damaged reef in Indonesia. The diverse reef in (b) may exhibit more varied responses to thermal stress, with some coral species experiencing bleaching and others relatively unaffected (as in the Indonesian reef in [d]).

effects of protective pre-bleaching exposure (Ainsworth *et al.* 2016), diurnal SST variability (Safaie *et al.* 2018), peak SST, thermal history, and duration of cool periods (McClanahan *et al.* 2019). Similarly, the wind-derived metrics of tropical cyclone intensity/category serve as typical surrogates to estimate coral reef damage, omitting size, duration, and translation speed measures to adequately quantify tropical cyclone-induced wave damage (Puotinen *et al.* 2020). Approaches that project ecological responses to future change showcase the best pathways for including ecological sensitivity in vulnerability assessments. These approaches should integrate a greater range of climate variables that dictate ecological responses and will often require regional specificity to effectively predict future ecological change.

Historical ecological responses to climate change are often determined by coral bleaching or growth responses (WebTable 1). Bleaching and growth provide indicators of climate sensitivity but do not account for the range of ecological responses that result from changes in environmental conditions (eg physical damage resulting from storms). Storms and bleaching events can result in coral mortality caused by sustained loss of symbionts and physical damage (Puotinen *et al.* 2016; Hughes *et al.* 2018), leading to a reduction in live hard coral cover. More gradual climatic changes (eg ocean warming) can influence coral growth and recovery, and impact competitive interactions between structurally complex hard coral and competing macroalgae (Anthony *et al.* 2015), which also influences hard coral cover. Measures of hard coral cover can capture ecosystem changes resulting from various stressors and the use of a single response variable allows comparison between different geographic locations. However, neither total nor single genera hard coral cover captures the difference in disturbance tolerance between organisms or changes in community composition following disturbance (Kim *et al.* 2019). Hard coral cover for the range of species/genera present at a location is necessary to indicate ecological change due to climate exposure. Currently, these responses to multiple climatic disturbances are difficult to quantify because of the lack of long-term data and presence of multiple factors that affect coral reef sensitivity. Even though such detailed data collection is costly and time consuming, long-term datasets are increasingly needed to better understand the response of corals to climate stressors (Van Woesik *et al.* 2018; Darling *et al.* 2019; Donner and Carilli 2019).

When projecting ecological responses to climate stress, a reef's adaptive capacity must also be considered. Coral reefs can acclimate or adapt to climatic changes over time (Hughes *et al.* 2017a), but the extent to which (and how) coral reefs can adapt is not well known (Mumby *et al.* 2011). Thermal adaptation has been linked to various SST characteristics, such as heating rate (Middlebrook *et al.* 2010), diurnal variability (Safaie *et al.* 2018), and high historical chronic and acute thermal stress (Mumby *et al.* 2011). However, these studies do not account for variability in adaptive capacity between species subjected to the same thermal disturbance (Safaie *et al.* 2018) or external factors affecting a site's adaptive capacity (eg supply of coral recruits adapted to warmer environments; Matz *et al.* 2020). Because adaptation is not guaranteed in locations that have been affected by past bleaching events (Hughes *et al.* 2017b), thermal regimes alone cannot provide a proxy for adaptive capacity in the identification of low vulnerability areas.

Long-term hard coral cover datasets that track past ecological responses of coral genera to multiple disturbances can facilitate identification of increasing resistance (or the lack thereof) for coral genera over time. Sites subjected to frequent disturbance – for instance, the high thermal stress exposure of the Gilbert Islands in Kiribati (Donner and Carilli 2019) or coral communities that currently exist under marginal environmental conditions resulting from multiple stressor types, such as macrotidal or upwelling reef environments (Camp *et al.* 2018) – are ideal candidates for monitoring changes in response to frequent exposure. Utilizing paleoecological data and further extending existing genus-level records for hard coral cover to track responses to consecutive disturbances over multiple locations, habitat types, and disturbance regimes will be vital for informing potential adaptive predictions of future ecological vulnerability.

Conclusions

The loss in coral reef value with continued ecosystem decline will impact millions of people who rely on the services coral reefs provide for their livelihoods (Hughes *et al.* 2017a). Our framework identifies low vulnerability areas for conservation using an ecologically sensitive, multi-stressor climate vulnerability measure. We recommend that this framework be implemented in climate vulnerability assessments to improve the use of climate model projections in conservation science. Ecologically informed climate vulnerability estimates can direct local-scale management efforts in identifying protected areas with the highest chance of reef survival, and assist international climate policy by quantifying future changes in coral reef ecosystems resulting from multiple interacting climate stressors. In future work, ecologically informed reef vulnerability can be used to predict how reefs might be transformed in terms of total and genera-level cover, and the contribution of adaptive capacity in maintaining coral cover. However, the role of vulnerability in guiding conservation requires a clear understanding of the management actions to be implemented alongside dedicated efforts to curtail global GHG emissions (Hughes *et al.* 2017a).

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