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RESEARCH ARTICLE

Regional and global climate risks for reef corals: Incorporating species-specific vulnerability and exposure to climate hazards

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Abstract

Climate change is driving rapid and widespread erosion of the environmental conditions that formerly supported species persistence. Existing projections of climate change typically focus on forecasts of acute environmental anomalies and global extinction risks. The current projections also frequently consider all species within a broad taxonomic group together without differentiating species-specific patterns. Consequently, we still know little about the explicit dimensions of climate risk (i.e., species-specific vulnerability, exposure and hazard) that are vital for predicting future biodiversity responses (e.g., adaptation, migration) and developing management and conservation strategies. Here, we use reef corals as model organisms ($n = 741$ species) to project the extent of regional and global climate risks of marine organisms into the future. We characterise species-specific vulnerability based on the global geographic range and historical environmental conditions (1900–1994) of each coral species within their ranges, and quantify the projected exposure to climate hazard beyond the historical conditions as climate risk. We show that many coral species will experience a complete loss of pre-modern climate analogs at the regional scale and across their entire distributional ranges, and such exposure to hazardous conditions are predicted to pose substantial regional and global climate risks to reef corals. Although high-latitude regions may provide climate refugia for some tropical corals until the mid-21st century, they will not become a universal haven for all corals. Notably, high-latitude specialists and species with small geographic ranges remain particularly vulnerable as they tend to possess limited capacities to avoid climate risks (e.g., via adaptive and migratory responses). Predicted climate risks are amplified substantially under the SSP5-8.5 compared with the SSP1-2.6 scenario, highlighting the need for stringent emission controls. Our projections of both regional and global climate risks offer unique opportunities to facilitate climate action at spatial scales relevant to conservation and management.

KEYWORDS

climate change, climate change vulnerability, climate risk assessment, coral, novel climate

1 | INTRODUCTION

Global biodiversity is suffering constant decline (Butchart et al., 2010). Anthropogenic habitat loss, overexploitation, pollution and proliferation of invasive species have been considered the primary causes of recent biodiversity loss, but climate change and its detrimental synergy with other factors are rapidly becoming the leading agents of global biodiversity decline (Arneth et al., 2020; Díaz et al., 2019). The pervasive impacts of climate change on global biodiversity and its economic and ecological implications (Pecl et al., 2017) have prompted multiple approaches to quantify and forecast climate change impacts on biodiversity (Araújo et al., 2019; Foden et al., 2019; Pacifici et al., 2015).

Analyses of climate change impacts frequently adopt the framework and guidelines devised by the Intergovernmental Panel on Climate Change (IPCC) to quantify risks of climate change. The current framework introduced in the 6th IPCC report recognises that the risk of climate change for a species is a function of intrinsic vulnerability and exposure to extrinsic climate hazards (Figure 1; IPCC, 2022). Climate risks can be indeed reduced by species responses, including adaptation, migration and behavioural modifications (Nogués-Bravo et al., 2018), yet the root causes of climate risks continue to escalate and threaten global biodiversity (Arneth et al., 2020; Butchart et al., 2010; Díaz et al., 2019). The need and demand for climate risk assessment are therefore higher than ever to identify threatened species and regions (Araújo et al., 2019; Foden et al., 2019). In particular, climate risks among habitat-forming species require urgent attention as they often exhibit higher vulnerability to climate change than other species, and their loss can lead to ecosystem collapse (Hobbs et al., 2018; Steneck et al., 2013; Wernberg et al., 2016).

Reef corals of the order Scleractinia comprise over 800 species globally (DeVantier & Turak, 2017; Veron et al., 2009, 2015). They create a complex habitat framework that sustains one of the most speciose ecosystems (Done, 1992; Done et al., 1996). Despite their ecological significance, coral species are declining in response to global warming and recurrent climatic and anthropogenic disturbances (Dietzel et al., 2021; Hughes et al., 2017, 2018; Kleypas et al., 2021). Projections of climate change impacts on corals tend to employ an approach unique to the group and focus on predictions of mass bleaching events that can lead to widespread mortality of corals. To date, climate risks for reef corals have been typically assessed based on spatially variable exposure of corals to climate hazards without considering species-specific climate sensitivity or adaptive capacity. Nevertheless, evidence suggests that climate sensitivity and adaptive capacity (i.e., vulnerability) vary among coral species and their associated symbionts (Howells et al., 2020; Kim et al., 2019; Loya et al., 2001; Sampayo et al., 2008; Sully et al., 2019; van Woesik et al., 2011). Indeed, a comprehensive climate risk assessment of coral species incorporating both the intrinsic vulnerability and exposure to extrinsic climate hazards can provide valuable insights into the degree to which reefs and coral taxa are at risk. Such comprehensive information can also enable more realistic predictions of coral community dynamics under climate change.

Here, we provide a climate risk assessment of 741 scleractinian coral species across the globe using metrics that incorporate the

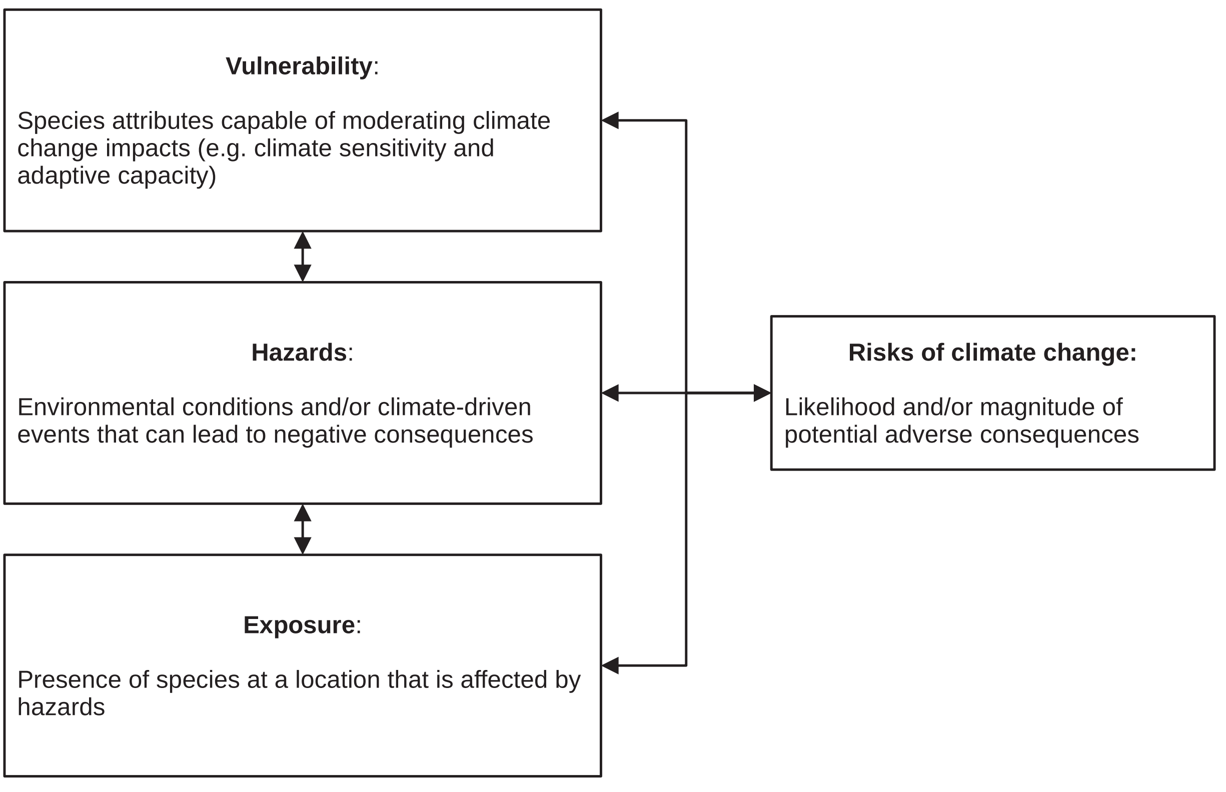

FIGURE 1 Dimensions of the 6th IPCC climate risk assessment and definitions adopted in this study (IPCC, 2022).

dimensions of the climate risk assessment framework of the 6th IPCC report (i.e., vulnerability, exposure and hazard; IPCC, 2022). To achieve this, we first evaluate species-specific environmental vulnerability based on the species' global geographic ranges and the historical environmental conditions therein. We then use a range of climate change trajectories to project the extent of future exposure to climate hazards. Our goal is to summarise the magnitude of potential adverse impacts of progressive climate change on reef corals. We aim at achieving this goal by understanding the discrepancy between the environmental vulnerability of each coral species and their future exposure to climate hazards, expressed as regional and global climate risks.

2 | MATERIALS AND METHODS

2.1 | Measuring the risk of climate change: Taxon-specific vulnerability

Our approach to climate risk assessment is based on a comparison between species-specific measurements of climate vulnerability and future exposure of species to climate hazards. Vulnerability is the capacity of a species to persist in a range of climate conditions, which often requires an explicit understanding of species traits (Williams et al., 2008). Unfortunately, the central repository for coral species traits still lacks a large amount data despite arduous efforts (Madin, Anderson, et al., 2016; Madin, Hoogenboom, et al., 2016). Alternatively, we use the association between georeferenced occurrence data and historical environmental conditions therein to define environmental conditions that support species persistence (Araújo & Peterson, 2012; Elith & Leathwick, 2009) and as a proxy to quantify climate vulnerability of each coral species. Vulnerability of each coral species was determined by characterising a multidimensional space that captures the species' past environmental exposures, combining two types of raw data: species occurrence and past information on environmental conditions (Figure S1).

The global coral species occurrence data were gathered from Huang and Roy (2015); their data set is an ecoregion-scale compilation of shallow-water coral occurrence records from the literature and various global databases (Carpenter et al., 2008; Hughes et al., 2013; Veron et al., 2009, 2011). The mesophotic coral diversity that occurred beyond 40 m in depth was not included in this data set. Species occurrence data for new taxa (Baird et al., 2017; Schmidt-Roach et al., 2013) were added to the data set. Subsequently, the species pool was further restricted to taxa that occurred in more than three ecoregions ($n = 741$).

We used the sixth-phase products of the Coupled Model Intercomparison Project (CMIP6) to amass past environmental exposure data (Eyring et al., 2016). We selected the annual mean and variability (i.e., standard deviation) of environmental parameters that can induce critical climate risks to reef corals: sea surface temperature (SST) and partial pressure of carbon dioxide (pCO_2) (Hoegh-Guldberg et al., 2017). We used environmental conditions for the years between 1900 and 1994 (i.e., post-industrial, pre-modern period; hereafter pre-modern period; IPCC, 2022) to derive species-specific climate vulnerability. A multimodel ensemble mean of the four environmental parameters (i.e., mean and standard deviation of SST and pCO_2) was derived from three CMIP6 general circulation models (GCMs) to reduce model uncertainty (Table S1). We considered Shared Socioeconomic Pathways (SSPs) 1–2.6 and 5–8.5 scenarios for future environmental projections. Shared Socioeconomic Pathways are specific to the CMIP6, and each pathway projects a distinctive greenhouse gas concentration and socio-economic development trajectory (O'Neill et al., 2016). We considered the SSP1-2.6 as a projection that requires stringent emission controls to limit global warming to 2°C, and the SSP5-8.5 as a continuum of contemporary fossil-fuel development, coupled with energy-exhaustive social and economic trends (Riahi et al., 2017).

To quantify vulnerability of each coral species (see Figure S1 for the step-by-step illustration of vulnerability computation), environmental conditions between 1900 and 1994 were first extracted from the multimodel ensemble for all data points in ecoregion polygons where species occurrences were recorded. We restricted the ecoregions to coastal areas (within 25 km from coastlines and reef boundaries) using the Natural Earth's land and reef maps (http://www.naturalearthdata.com) prior to extracting environmental parameters to avoid the parts of ecoregions that are uninhabitable for reef corals (e.g., open ocean). The extracted environmental parameters were summarised by taking ecoregion-scale medians of the parameters for each coral ecoregion (Veron et al., 2009) to avoid potential disproportionate effects of environmental outliers. The taxon-specific compilation of ecoregion-scale environmental data was then transformed into two-dimensional data by calculating the first two principal components of the environmental variables using a principal component analysis (PCA; the first and second PC axes captured over 85% of the total variation in environmental conditions for scleractinian corals). The multidimensional space occupied by taxon-specific environmental coordinates is equivalent to the species' historical climate exposure between 1900 and 1994, or its 'vulnerability'. To render vulnerability into an enclosed space with explicit boundaries for downstream analyses, we defined a convex hull encompassing the coordinates (Figure S1) using the 'QUICKERSORT' algorithm implemented in the 'chull' function in base R (Eddy, 1977). 'Vulnerability' in this study shares its theoretical basis with environmental niche models and their synonyms (e.g., habitat suitability models, bioclimatic envelope models). The core difference between the vulnerability in this study and the niche space of other models lies in the interpretation of the multidimensional space boundaries. Here, we recognise the vulnerability hull as a reference environmental space in which organisms have avoided vulnerable conditions prior to the 'modern' period defined by the IPCC during and after which climate change intensified (IPCC, 2022). As such, the space outside the vulnerability hull provides critical information about the magnitude of environmental hazards caused by progressive climate change after the pre-modern reference period (1900–1994), while the same space would be considered uninformative in most environmental niche models.

We also estimated the range size of each species to test whether species with smaller range sizes were projected to experience greater climate risks than widespread species (Purvis et al., 2000; Rabinowitz, 1981). The range size of each species was estimated by summing the coastal and reefal areas within all ecoregions that each species was recorded in using the occurrence dataset and the Natural Earth's land and reef maps (http://www.naturalearthdata.com).

2.2 | Measuring the risk of climate change: Exposure to climate hazards

We used our measure of taxon-specific vulnerability (Figure S1) as the basis for two distance metrics that quantified taxon-specific exposure to climate hazards (Figure S2). First, we calculated the Euclidean distance between the taxon-specific centre of the vulnerability hull and the environmental coordinates of each species' occurrence record (hereafter the centroid distance or dC; Figure S2; Dallas et al., 2017; Kriticos et al., 2014). Second, we measured the radial distance between the centroid and the nearest edge of the species' vulnerability hull via the environmental coordinates of the species' occurrence record (hereafter the edge distance or dE; Figure S2). We then computed the ratio between the edge and the centroid distances (i.e., dE/dC; Figure S2). We refer to the logarithmic transformation of this ratio as the 'multidimensional Climate Risk Score (mCRS)' throughout this manuscript. It is important to note that distances from environmental coordinates of a species' occurrence record to the vulnerability hull centre (i.e., environmental centrality) and boundaries (i.e., environmental marginality) are not necessarily correlated (Santini et al., 2019). mCRS captures both the centrality and marginality of coordinates of the study sites in relation to the species-specific vulnerability hull. The ratio between the edge and centroid distances (dE/dC) is 1 and the logarithmic transformation of this ratio ($\log(dE/dC) = mCRS$) is 0 when the coordinates of a study site are on the boundaries of a vulnerability hull. mCRS is greater than 0 when the coordinates of a study site occur within a vulnerability hull. mCRS is smaller than 0 when the coordinates of a study site are situated outside of a vulnerability hull. A mCRS value smaller than 0 only occurs when environmental conditions exceed the extent of a vulnerability hull that is constructed based on pre-modern environmental conditions (i.e., signifying exposure to climate hazards). This process was iterated over years between 1995 and 2100 to calculate annual climate risk at each occurrence location for each coral species. We also tested whether regional climate risk diminished towards the boundaries of the vulnerability hull to examine whether corals in historically marginal habitats will experience reduced climate hazards than in their preferred habitats over the modern and post-modern periods (1995–2100). All R scripts required to compute the mCRS and reproduce results of this study are shared in a data repository (doi: 10.5061/dryad.jh9w0vtgk).

2.3 | Interpretation of the mCRS metrics and caveats

In this study, we use the mCRS to infer two spatial aspects of climate risks. First, we use ΔmCRS to evaluate temporal changes in environmental conditions at a region by computing the difference in mCRS values of the same ecoregion over time (i.e., regional climate risk; e.g., $\Delta mCRS_{2100} = mCRS_{2100} - \mu mCRS_{\text{pre-modern period}}$). A more negative ΔmCRS value indicates a greater departure from a set of environmental conditions that historically supported the regional population (Figure S1) and implies a higher likelihood/magnitude of adverse implications for the regional population. Second, we use mCRS values to identify the emergence of global climate risk. By design, a negative mCRS value at a location in a given year indicates that environmental conditions have exceeded conditions that the species experienced at any location across its entire distributional range in the past (i.e., the 6th IPCC pre-modern period: 1900–1994; IPCC, 2022), likely leading to substantial loss of the species' capacity to persist without dramatic responses.

The design of our risk framework includes few assumptions and caveats. First, our designation of reference period to define the species-specific vulnerability may render the risk scores sensitive. Indeed, many reef coral species thrive under post-modern environmental conditions, suggesting that the fundamental species-specific vulnerability spaces may be generally larger than those defined in this study. However, the inclusion of modern and/or post-modern environmental conditions would reduce the sensitivity of our risk scores and weaken the scores' capacity to detect regional and global risks stemming from progressive climate change that intensified after the reference period (IPCC, 2022). Second, we focus on the projected persistence of reef corals within their current geographic ranges and do not account for potential biological and ecological processes that can reduce climate risks (e.g., adaptation and migration) due to the critical lack of data on the rate and magnitude of these processes for each coral species. Third, our metrics of climate risks assume a uniform decay of vulnerability from the hull centre to the boundaries because species-specific fitness kernels for our environmental parameters are not generally available for most scleractinian corals, and the available kernels are taxonomically biased (Madin, Anderson, et al., 2016; Madin, Hoogenboom, et al., 2016).

3 | RESULTS

3.1 | Regional and global climate risks for scleractinian corals

Regional climate risk (ΔmCRS; climate risk to a species at a location from changes in regional environmental conditions that can alter persistence at the location) is already widespread across coral taxa in 2023 and is rapidly escalating (Figure 2a,b; annual results for full species list in Table S2). The discrepancy in regional climate risks between the SSPs is projected to widen towards the end of

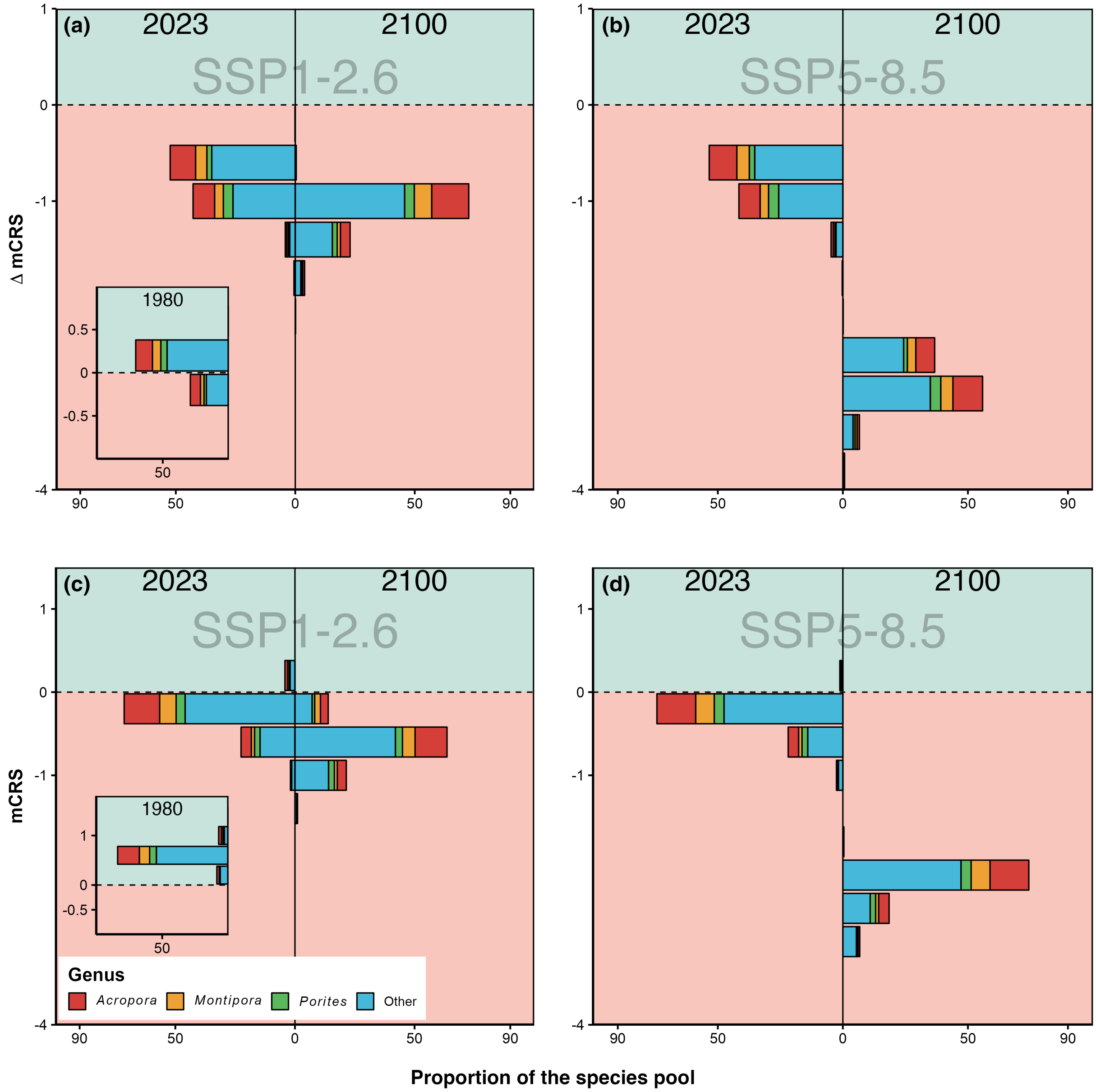

FIGURE 2 Projected (a, b) regional (ΔmCRS) and (c, d) global (mCRS) climate risks for reef corals under the two CMIP6 trajectories (SSP1-2.6, SSP5-8.5). Species-specific mCRS and ΔmCRS values were summarised by calculating species-specific annual medians of mCRS and ΔmCRS values. Histogram bins were generated by sectioning the mCRS and ΔmCRS value ranges into 0.4-width bins. Positive values of each plot (top panels—green background) indicate (a, b) an absence of regional climate risks and (c, d) a presence of pre-modern (1990–1994) environmental conditions within the species' current global distribution. Negative values of each plot (bottom panels—red background) indicate (a, b) a regional escalation in climate risks since the pre-modern reference period and (c, d) an absence of pre-modern environmental conditions within the species' range. Plots in the first and second columns show patterns under the SSP1-2.6 and SSP5-8.5 scenarios, respectively. Bar plots in the left and right-hand panels of each column illustrate patterns projected for 2023 and 2100, respectively. Inset plots in (a, c) show regional and global climate risks computed for one of the pre-modern period years, 1980. Numbers in all plots indicate the proportion of the total observations (%) under each quadrant's climate trajectory and climate risk category. Numbers are rounded to the nearest integer.

the century. Regional climate risks are predicted to pose substantially greater threat under the SSP5-8.5 scenario compared with the SSP1-2.6 scenario (Figure 2a,b). We also found that regional climate risk was predicted to decline towards the boundaries of the vulnerability hull where environmental conditions would be considered marginal in the past (Pearson's ρ between the distance to vulnerability hull boundaries (i.e., dE − dC) and regional climate risk (ΔmCRS); $\rho = -0.88$, $p < .01$ for SSP1-2.6; $\rho = -0.94$, $p < .01$ for SSP5-8.5; Figure S3; Table S3).

Global climate risk (mCRS; climate risk to a species at a location from an exposure to environmental conditions that are completely dissimilar to pre-modern conditions across the species' entire geographic range) is also exacerbated over time and shows a clear disparity between the two SSP scenarios (Figure 2c,d). There are still locations in 2023 that can provide corals with pre-modern (1900–1994) environmental conditions (green background in Figure 2c,d). These locations are mostly situated in the northern hemisphere, and the extent of global climate risk tends to decrease towards high latitudes (Figure S4). Nonetheless, these temporary climate refugia are rare and predicted to vanish in the near future (red background in Figures 2c,d and 3).

Analysis of projected regional and global climate risks divided corals at a location into two groups. The first group is characterised by negative ΔmCRS and positive mCRS values. Corals with these risk outcomes at a location experience less favourable environmental conditions than during the pre-modern period at the location (i.e., negative ΔmCRS; regional climate risk). Despite the presence of regional climate risk, the location still provides environmental conditions within the range of pre-modern conditions that the species has experienced elsewhere within its distributional range in the past (i.e., positive mCRS). Only a small portion of the examined corals experience these conditions today (4.2% under the SSP1-2.6 in 2023; 1.2% under the SSP5-8.5 in 2023; Table S4). The second group of corals displays negative values for both ΔmCRS and mCRS metrics. These values highlight regional degradation of environmental conditions and a complete loss of potential climate refugia with pre-modern environmental conditions within the current species range. All examined taxa were projected to experience these risks by the end of the century regardless of the Shared Socioeconomic Pathway (SSP, Table S4) considered in the analyses. Species-level differences in climate risks were widespread (Table S2), and each genus included species with wide ranges of regional and global climate risks (Figure S5).

3.2 | Geographic patterns of climate risks for scleractinian corals

Although risk magnitude varies across space, corals already experience considerable regional and global climate risks today (Figures 3 and 4). As environmental conditions are rapidly becoming dissimilar to the pre-modern conditions, corals are facing extensive global climate risk (Figure 3). The onset of global climate risk is delayed in the northern hemisphere, particularly at high latitudes (Figure 3). At higher latitudes, corals are also exposed to lower regional climate risks than in the tropics (Figure 4). These spatial differences in the level of regional and global climate risks diminish under the higher emissions scenario (Figures 3 and 4). Indeed, by mid-century, there is no place where corals will be able to avoid global climate risk under the SSP5-8.5 (Figure 3b). Importantly, comparison among coral species showed that small-range species will experience greater global climate risks than widespread species, a pattern that is further exacerbated under the higher emissions scenario (Figure S6; Table S6).

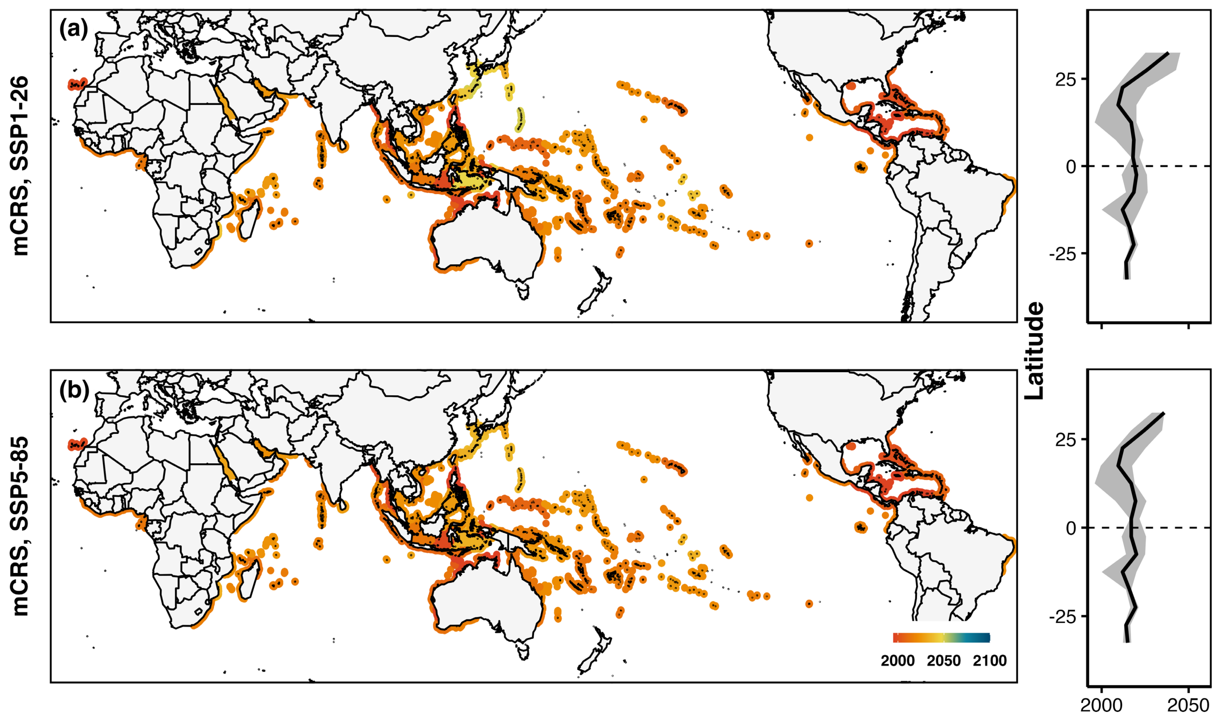

FIGURE 3 Timing of global climate risk (mCRS) for reef corals under the (a) SSP1-2.6 and (b) SSP5-8.5 scenarios. The values on the map and marginal panels to the right show the regional and latitudinal median year in which species-specific mCRS values turn negative (i.e., hazardous climate for all species or the emergence of global climate risk across taxa within the region; solid lines in the marginal panel) and the first and third quartiles of the year in which global climate risk emerges (shaded areas in the marginal panel). Data are only shown in the coastal zone of each ecoregion. Map lines do not necessarily depict accepted national boundaries.

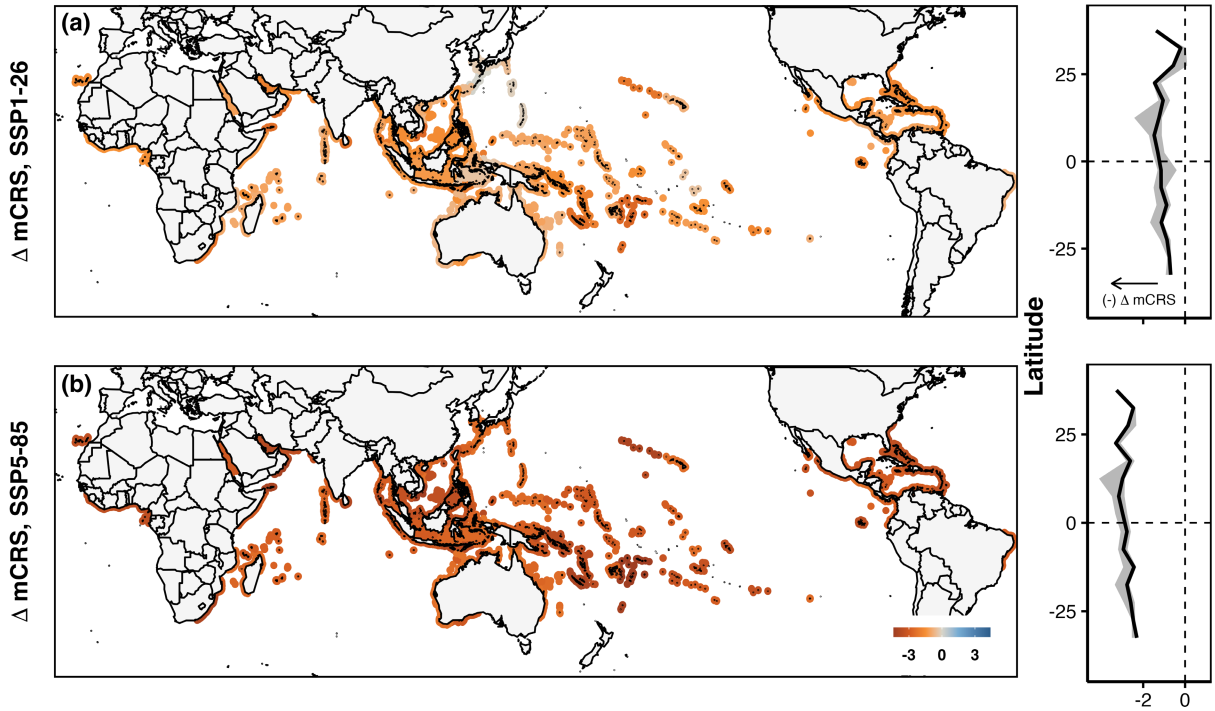

FIGURE 4 Geographic patterns of projected regional climate risks (ΔmCRS) for reef corals in 2100 under the (a) SSP1-2.6 and (b) SSP5-8.5 scenarios. The marginal panels to the right show the latitudinal median of species-specific regional climate risks (solid lines) and the first and third quartiles of the ΔmCRS values (shaded areas). A negative ΔmCRS value at a location indicates that regional climate risk is common across coral taxa at the location. Data are only shown in the coastal zone of each ecoregion. Map lines do not necessarily depict accepted national boundaries.

4 | DISCUSSION

Our findings foreshadow marked and continuous escalation of both regional and global climate risks for reef corals over the course of this century. Regional environmental conditions have already exceeded the range of pre-modern environmental conditions for all coral species (i.e., regional climate risk), even under stringent emission controls (i.e., SSP1-2.6; Figure 2a). Moreover, regional climate risks are projected to intensify rapidly in the future (Figures 2a,b and 4), consistent with widespread predicted losses of local/regional thermal refugia based on current understanding of reef corals' generic thermal tolerance (Dixon et al., 2022). These findings highlight the severity of climate change impacts at regional scales, rapidly forcing corals to move to new locations within or outside their current distributional ranges (Cacciapaglia & Woesik, 2015; Couce et al., 2013; Descombes et al., 2015) or to adapt to the new conditions in situ (Bairos-Novak et al., 2021).

From a conservation and management perspective, the existence of climate refugia within a species' current distribution offers opportunities for active intervention approaches that can alleviate global climate risks (but see Chen et al., 2022; Rinkevich, 2021 for a list of caveats). Nevertheless, our findings only detected few climate refugia within the current species ranges of reef corals today and in the near future (Figures 2c,d and 3; Figure S4). These temporary refugia are located in the northern hemisphere, often at high latitudes (Figure S4). At these locations, environmental conditions still remain within the range of pre-modern conditions. Assuming little influence of adaptation, migration of individuals/populations to these locations may reduce global climate risks. However, reef corals are sessile organisms whose structural formation takes years to centuries (Done, 1987), and rates of their range expansions (Yamano et al., 2011) are unlikely to outstrip the projected increase in global climate risk (Figure 3). Under these pressing circumstances, ex situ (i.e., outside a species' current range) responses (Chen et al., 2009; García Molinos et al., 2016; Johnson et al., 2011; Last et al., 2011; Lenoir & Svenning, 2015; Moritz et al., 2008; Pinsky et al., 2013; Thomas & Lennon, 1999; van Herk et al., 2002; Whitfield et al., 2007) and associated conservation strategies (Rehfeldt & Jaquish, 2010; Williams & Dumroese, 2013) might be necessary, as in situ (i.e., within a species' current range) responses other than extirpation may become unlikely (Morelli et al., 2020; Potter & Hargrove, 2012).

Our study provides important insights to clarify the degree to which high-latitude regions will provide climate refugia for scleractinian corals (Glynn, 1996). High-latitude regions have served corals as climate refugia in both historical and contemporary records. Tropical corals shifted their geographic ranges towards high latitudes during warmer climatic periods, such as the Last Interglacial of the Pleistocene (Greenstein & Pandolfi, 2008; Kiessling et al., 2012). Poleward range expansions of corals are also observed in many regions today (Baird et al., 2012; Denis et al., 2013; Marsh, 1993; Precht & Aronson, 2004; Yamano et al., 2011). Our results suggest that high-latitude regions are likely to pose less climate risk to tropical corals

(Figure 3; Figure S3), especially if corals are capable of migrating beyond their current geographic ranges (but see Abrego et al., 2021 for drivers limiting latitudinal distribution of reef corals including various physical and biotic factors). On the contrary, current high-latitude residents are projected to suffer substantial regional climate risks akin to tropical corals in the tropics (Figure 4). In other words, high-latitude regions will not become generic climate refugia for all corals. Rather, they will only provide viable habitat for tropical corals whose pre-modern conditions in the tropics will resemble those at high latitudes in the future. Unlike their tropical counterparts, successful poleward range shifts of high-latitude specialists may be limited as they already exist under physical and biological stresses (Harriott & Banks, 2002; Kleypas et al., 1999; Sommer et al., 2018), and habitable substrates may be unavailable at high latitudes (Beger et al., 2014; Harriott & Banks, 2002; Kawecki, 2008; Lybolt et al., 2011; Perry & Larcombe, 2003). Moreover, mounting evidence suggests that subtropical specialists and endemics are particularly vulnerable to heat stress and coral bleaching (Cant et al., 2021; Kim et al., 2019; Lachs et al., 2021). Similar to observations among other flora and fauna (Jablonski, 2008; Parmesan, 2006), many high-latitude corals may thus experience contractions of their geographic ranges and greater extinction risk as their environmental conditions become unfavourable under climate change, and/or they are unable to compete with local species and incoming vagrants.

Importantly, our results also highlight the vulnerability of coral species with small-range sizes (Figure S6; Table S6). Small-range coral species are projected to experience higher global climate risks compared with widespread taxa, such that greater extents of novel climate conditions will engulf their entire distributional ranges. Notably, coral species with small ranges did not cluster in particular genera (Figure S7), indicating that climate risk associated with small species ranges is broadly distributed across coral genera. Although many coral species are geographically widespread and the number of small-range species is relatively low (Hughes et al., 2002, 2013), their disproportionate exposure to climate change is concerning. Dependence of these small-range species on a restricted number of disappearing habitats and refugia is likely to make them particularly vulnerable to climate change (Murali et al., 2021; Purvis et al., 2000; Trew & Maclean, 2021). For example, terrestrial regions with small-range species are predicted to experience approximately 1.2 times faster rates of global warming and 1.6 times higher anthropogenic impacts, severely threatening their persistence (Enquist et al., 2019). Moreover, small-range species often perform important functions (e.g., provision of complex habitat by the branching endemic *Pocillopora aliciae* on temperate reefs; Booth & Sear, 2018), and the loss of geographically rare species (Rabinowitz, 1981) can impair novel or important ecological interactions and ecosystem processes (Gorman et al., 2014; Mouillot et al., 2013; Valiente-Banuet et al., 2015).

Evidence is clear on the pervasive impacts of climate change across many elements of biodiversity (Bellard et al., 2012; Shin et al., 2019). A perilous number of organisms across terrestrial and marine realms are predicted to suffer critical climate risks and lose suitable habitats by the end of the century (García Molinos et al., 2016; Segan et al., 2016). Scleractinian corals are no exception. Consistent with the notion that climate change will escalate extinction risks for corals (Finnegan et al., 2015; Hughes et al., 2017; Kornder et al., 2018; Pandolfi et al., 2011; van Hooidonk et al., 2016), our findings indicate that the business-as-usual climate trajectory (i.e., SSP5-8.5; but see Hausfather & Peters, 2020) will put all corals at critical risk. Our results also highlight added climate risks for high-latitude specialists and small-range taxa, as their traits and local environmental conditions tend to restrict opportunities for adaptation and migration (Trew & Maclean, 2021). While the spatial variability in predicted climate risks among coral taxa points to considerable reorganisation of coral assemblages on regional to global scales, our findings also emphasise that climate risks can be reduced by stringent climate actions (i.e., SSP1-2.6 vs. SSP5-8.5). In addition, evidence suggests that corals are actively employing response strategies, such as adaptation and range shifts, to reduce climate risks (e.g., Matz et al., 2018; Tuckett et al., 2017). These findings highlight the utility of current and anticipated emission controls and reinforce hope in climate actions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

This study used data available in the literature and public domain. The data that support the findings of this study are available in Dryad at https://doi.org/10.5061/dryad.jh9w0vtgk. Environmental data that support the findings of this study were obtained from the sixth phase of Coupled Model Intercomparison Project (https://esgf-node.llnl.gov/projects/cmip6/). All scripts to replicate the findings of this study are also uploaded on Dryad at https://doi.org/10.5061/dryad.jh9w0vtgk.

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