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Future climate warming threatens coral reef function on World Heritage reefs

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Abstract

Climate change is the most significant threat to natural World Heritage (WH) sites, especially in the oceans. Warming has devastated marine faunas, including reef corals, kelp, and seagrass. Here, we project future declines in species and ecosystem functions across Australia's four WH coral reef regions. Model simulations estimating species-level abundances and probabilities of ecological persistence were combined with trait space reconstructions at "present," 2050 (+1.5°C of warming), and 2100 (+2°C) to explore biogeographical overlaps and identify key functional differences and forecast changes in function through time. Future climates varied by region, with Shark Bay projected to warm the most (>1.29°C), followed by Lord Howe, when standardized to marine park size. By 2050, ~40% of the Great Barrier Reef will exceed critical thresholds set by the warmest summer month (mean monthly maximum [MMM]), triggering mortality. Functional diversity was greatest at Ningaloo. At +1.5°C of warming, species and regions varied drastically in their functional responses, declined 20.2% in species richness (~70 extinctions) and lost functions across all reefs. At +2°C, models predicted a complete collapse of functions, consistent with IPCC forecasts. This variability suggests a bespoke management approach is needed for each region and is critical for understanding WH vulnerability to climate change, identifying thresholds, and quantifying uncertainty of impacts. This knowledge will aid in focusing management, policy and conservation actions to direct resources, rapid action, and set biodiversity targets for these reefs of global priority. As reefs reassemble into novel or different configurations, determining the winners and losers of functional space will be critical for meeting global landmark biodiversity goals.

KEYWORDS
climate change, coral reef, extinction, function, warming, World Heritage areas

1 | INTRODUCTION

Human-driven climate warming induces multiple response pathways in organisms, including migration, acclimation, adaptation, or extinction. As climate patterns change over time, including drought, flooding, and coral reef bleaching, coping responses must increase rapidly to ensure population persistence. In the short term, species can disperse (Pinsky et al., 2020) and move into new environments

rapidly at the leading edge of habitats or the margin of a dispersal envelope, or they may occupy a wider niche space (i.e., functional trait space). Over longer evolutionary time scales, selective forces, like directional selection, can modify the fitness landscape such that new areas of niche space become occupied (Munoz et al., 2023). The confluence of these dynamic responses will be challenging for managers of marine protected areas—although other ecosystems may offer insights into to the benefits of long-term adaptive protection (Laurance et al., 2012). In response, the borders of conventional management could shift as the needs of systematic conservation planning become increasingly dynamic. Ultimately, halting biodiversity loss globally will need to consider short- and long-term impacts occurring inside and outside protected areas.

Ocean temperatures are already the dominant driver of adaptation in the oceans (reviewed in Liggins et al., 2020), and warming is causing further pressure. Extreme weather driven by climate change is the principal (Heron et al., 2017; Lin et al., 2023) and fastest (Osipova et al., 2017) growing threat to natural World Heritage (WH) sites globally and across Australia. This includes coral reefs. At +1.0–1.5°C of warming, coral reefs are already at risk of partial and large-scale mortality events (measured as changes in habitat or coral cover), which could lead to loss of ecological functions, and by +2°C, this risk grows significantly (Cacciapaglia & van Woesik, 2020; Frieler et al., 2013; Schleussner et al., 2016). Although the estimates of the magnitude of change on reefs varies across different metrics and measurement techniques (Klein et al., 2024), future outlooks for reefs are worrying. For example, in response to disturbance, we know that historical and present-day ecological changes at the functional level include shifts to groups of taxa with limited functions relative to pre-disturbance, despite recovery in coral cover (McWilliam et al., 2020). Understanding the ecological changes—especially at the functional level—brought on by increasing temperature is critical for forecasting reef futures. However, it is currently unknown which reefs are most at risk and how reef functional diversity will be impacted.

Of Australia's 20 recognized WH sites, four are coral reef areas of outstanding universal value to humanity: the Great Barrier Reef (GBR), Ningaloo, Shark Bay, and Lord Howe Island (LHI). Degradation of reefs at these sites risks the loss of WH status for failure to maintain "conditions of integrity." Given many corals exist within 1–2°C of their upper thermal threshold (Berkelmans & Willis, 1999), this leaves little additional temperature increase before stress thresholds are reached. Corals are therefore at the climate frontline and as climate change accelerates, the result will be the loss of biodiversity, ecosystem services, and the erosion of cultural heritage values. With this, varied predictions of reef futures under climate change exist and range from some reefs serving as refuges while others are at risk (Klein et al., 2024). These include reefs that have naturally resilient populations (Quigley, 2024) or have escaped bleaching due to favorable hydrodynamic conditions (Beyer et al., 2018). Although previous assessments show general historical declines in reefs across Australia (Edgar et al., 2023; Hughes et al., 2018), they have not been assessed at the WH management level or for ecological function.

Coral reef regions across the Australian continent are likely to be responding differently to climate change. Globally iconic Australian WH reefs, like the GBR, have received widespread coverage of the damage caused by coral bleaching (Hughes et al., 2018). Relatively less is known about the world's longest fringing reef, Ningaloo, along the Western Australian coastline, and low latitude reefs, like Shark Bay and LHI, the most southern coral reef in the world. Adaptive genetic responses to warming are expected to be particularly urgent (Pinsky et al., 2023) given corals cannot infinitely "move" (Booth & Sear, 2018). For example, at LHI, there is limited evidence for extension beyond their southern limits in the Tasman Sea or along the coast or to adjacent sea mounts. Western Australian reefs are at particular risk as warming hotspots with the potential for high endemicity, although this is not currently understood for corals. Indeed, Shark Bay has experienced the most severe historical and recent stress among the four WH locations (>6 bleaching events/decade), followed by the GBR, Ningaloo, and LHI (Edgar et al., 2023; Heron et al., 2017). None have escaped heat stress completely.

As ecosystems change, it will be critical to predict species loss and gain across ecosystems. Increasingly, there is potential for species to emerge into novel habitats or alternatively, for species boundaries to decrease, potentially reflecting the heterogeneous nature of reefs given their habitat complexity, varied stressors and numerous engineering species that create functional space for others to evolve (Greenstein & Pandolfi, 2008; Munoz et al., 2023). Understanding functional changes with shifts in species assemblages will be increasingly important (Streit & Bellwood, 2023). Evidence of functional changes within species assembles have been documented in corals (McWilliam et al., 2020). These changes include both the functionally unique species (species responsible for relatively rare functions) as well as functionally dissimilar species (species responsible for functions that are highly distinct). Over time, changes may also include the formation of unique functions, the development of alternative strategies for survival within equivalent functional envelopes and evidence of storage effects—which describes functionally unique species ("eccentric peaks" sensu Munoz et al., 2023). In a fitness landscape perspective, these unique species occur at the major fitness peaks across habitats (i.e., those that make up the core of species assemblages in a functional trait distribution across diverse habitats). The depletion of these functionally similar species across regions would likely cause knock-on effects and radically change these ecosystems. The identification of such species is critical to managing resilient, healthy ecosystems, including those on WH reefs.

Extinction rates are estimated to be 100× greater now relative to geological time (Ceballos et al., 2017), so forecasting how ecosystems will function in the future will be the critical question. The concept of extinction can be generalized into ecological, functional, or numerical extinction. Here we focus on the impacts of species loss from an ecological and functional perspective, and acknowledge that numerical extinctions will likely take much longer given the spatial, interspecific, and intraspecific variability in warming trajectories. Taking a functional perspective will require looking beyond just

species extinctions (Streit & Bellwood, 2023). Indeed, the interest in defining functions on reefs has grown with new frameworks (Brandl et al., 2019; Darling et al., 2012; Kuo et al., 2023; Madin et al., 2016; McWilliam et al., 2018), including functional approaches applied to fish (Streit & Bellwood, 2023), corals (Madin et al., 2016; McWilliam et al., 2018), and coral's dinoflagellate symbionts (Terrell et al., 2021). Therefore, an understanding of function and the drivers of speciation and uniqueness are critical to predicting species composition and functional changes as corals continue to accommodate rapidly warming waters (Streit & Bellwood, 2023).

To inform these potentially large-scale shifts, we applied a functional trait space approach to predict species assemblages and the functional space presently occupied and forecasted under multiple future warming scenarios across all four of Australia's World Heritage protected reef regions. We identified species with unique and species with overlapping functions across regions and quantified predicted functional losses and collapse under scenarios of climate change. Information on the ecological persistence of species and functions should be a part of every climate readiness plan, especially for habitats already threatened (Hoeppner & Hughes, 2019).

2 | METHODS

2.1 | Overview

We estimated the likelihood of persistence of each species by first collating data on their respective regional abundances, which we then projected into the future based on estimates of heat stress-induced long-term changes in coral cover (Figure S1). We did this by (a) collating data on regional coral abundances per WH region, (b) calculating the return frequency of heat stress events under two climate change scenarios (1.5 or 2°C increase), and (c) the expected rate of change in coral cover across Australia. In addition to the estimated changes in coral cover, the ecological persistence metric also included coral life-history characteristics (abundances relative to changes in coral cover, range size, and bleaching susceptibility). If a species' relative abundance drops below zero, it is assumed to have gone extinct. Functional trait space was then calculated for each World Heritage region based on these outputs for each warming scenario.

2.2 | Functional trait space approach and groupings

Here, we define functional traits as those that are useful for predicting ecological outcomes (sensu Streit & Bellwood, 2023). Functional traits included here were taxonomy, range size, local abundance, bleaching susceptibility, typical growth form, and a range of phenotypic measurements (e.g., growth rate, corallite width) (Madin et al., 2016), as described by Madin et al. (2021) and McWilliam et al. (2018). These traits were then categorized into broader groups, including Goreau's 1963 framework of cementers,

fillers, and builders, life-history categories (generalist, competitive, stress-tolerant, weedy) (Darling et al., 2012), and Veron's families (Veron, 2000) (see comparative example in Madin et al., 2021). We will focus on Goreau's framework that includes species that create reef structure (builders), fill in remaining space (fillers) or connect parts of the reef together (cementers). These categories were quantitatively defined by growth rate, corallite width, rugosity/branch spacing, surface area per unit volume, colony height, maximum colony size/diameter, and skeletal density as per McWilliam et al. (2018). This framework allows for the identification of species with low and high functional distinctiveness or those that share high overlap with other species in trait space (average phenotypes, sensu Munoz et al., 2023).

The species lists were originally compiled from Huang and Roy (2015) and McWilliam et al. (2018). Some species were present in Huang and Roy (2015), but not in the more recent (McWilliam et al., 2018), so the more recent (McWilliam et al., 2018) list was used. Overall, the species lists from McWilliam et al. (2018) were updated to currently accepted species names via the World Register of Marine Species register (WoRMs) and reviewed for any differences. Specifically, this included removing species that were present in Huang and Roy (2015), but not in McWilliam et al. (2018) ($n = 10$ for GBR, 4 for Ningaloo, 1 for LHI, 3 for Shark Bay), updating taxonomic species names to those available at WoRMS ($n = 40$ for GBR, 29 for Ningaloo, 13 for LHI, 28 for Shark Bay) and spellings made consistent with the register ($n = 3$ total, $n = 2$ for GBR, 3 for Ningaloo, 1 for LHI, 3 for Shark Bay). Most names were consistent ($n = 369$ for GBR, 277 for Ningaloo, 62 for LHI, 248 for Shark Bay) and the final species lists were relatively unchanged. These taxonomic edits did not result in any species being split. Additionally, species lists for Ningaloo and Lord Howe Island were re-confirmed following consultation with co-authors currently undertaking taxonomic revisions at those specific locations (A.H. Baird). Information on the distribution of different species was then overlaid on each WH region. Species richness for each region was as follows: Shark Bay ($n = 251$), Ningaloo ($n = 283$), GBR ($n = 402$), and Lord Howe ($n = 112$).

Data were first collated on the regional abundances of each respective coral species from survey data from each individual WH region. Projected rates of coral cover changes per species per WH region were calculated using best available abundance data. These data represent the most up-to-date data across the greatest spatial extent within each region at the species level and are best characterized as a single "snapshot." The original analyses in Madin et al. (2021) utilized "abundance" data sourced from Veron (2000), in which global surveys were categorized to the species-level as "common," "uncommon," or "rare" and then converted into numerical bins ("1," "0.5," "0.25"). For our analyses here, we use relative abundances from empirical survey data from three sources. To convert survey data to relative abundances, these values were updated based on either the most recent monitoring data by state management authorities for Ningaloo and Shark Bay (Department of Biodiversity, Conservation and Attractions—DBCA, pers comms) or the most recent surveys for LHI (Keith et al., 2015) and the GBR (Kuo

et al., 2023). These survey data, however, were collected at different taxonomic levels. All relative abundance data sourced from DBCA monitoring data was available to the genus level for most taxa, or at times, to the family level. To convert these survey data and to ensure abundance estimates were standardized to an equivalent taxonomic level (e.g., to species), numerical transformations were applied as follows. Missing abundances at the species level were replaced with the mean from the nearest species as phylogenetic distance (i.e., closest genus or the overall family mean). For Shark Bay, four families were not detected and so did not have accompanying abundance data and were marked as NAs (*Plesiastreidae*, *Psammocoridae*, *Siderastreidae*, *Coscinaraeidae*). LHI and GBR data were available to the species level, although for the GBR some species were missing from surveys compared to the complete list from McWilliam et al. (2018). Missing data may represent rare species; however, this may also be due to differences in survey methods between the two studies. In this case, any missing species values were designated with mean abundance from the genus. The impact of averaging relative abundances on ultimate persistence predictions were investigated but did not significantly impact resulting functional analyses.

To calculate the expected rate of coral cover change with increasing temperatures, globally derived raw data were retrieved from González-Barrios et al. (2023). This data describes the mean annual rate of change for different reefs, relative to the degree heating weeks (DHW), accumulated during the measurement time periods of interest. Briefly, this open-source global analysis included 1000 time series from 136 studies, although thermal stress events for Australia made up a smaller proportion of this larger dataset ($n = 39$ of 1609 datapoints). These authors define change in coral cover as the annual rate of change in absolute cover between before and after a disturbance event, in-line with consistently used definitions in the literature. A linear regression was fitted to the extracted Australia-wide data to determine the relationship between predicted rate of change in coral cover and DHW ($-2.9 - (0.2 \times \text{DHW})$). For example, at 8 DHW (= or >2 degree heating months), the Australian wide rate of decrease for this measurement period was -4.5%. This was higher than the global mean (between -4.5% and -2.5%) from regions with similar coral cover that sustained equivalent thermal stress (González-Barrios et al., 2023) (Figure S2). Non-linear relationships and non-Australian reefs (explained below) were also included to explore how variation in estimates of coral cover may impact model outputs, although we found that these variations did not explain additional information relative to the simpler linear model (variation explained as R^2, Figures S3 and S4). These results incorporating other reefs (e.g., $y = -2 - 0.26x$, equivalent to -4.08% rate of decrease) were consistent with our Australian-only estimates (Figures S3 and S4). We therefore proceeded with our Australian-only estimates.

To estimate future increases in the frequency of heat stress events per WH region, the frequency of degree heating months (DHW) were extracted from Frieler et al. (2013) for $+1.5°C$ and $+2°C$. DHM has the units of DHM >2°C×months events (1 year^{-1}). To contextualize this, the >2°C×month metric can be used as an indicator of a severe bleaching event, equivalent to >8 DHW (Hughes et al., 2018), whereas a return frequency of 0.3 equates to severe bleaching once every 3 years (see LHI warming 1.5°C of warming scenario). To calculate frequencies, these authors use three different global mean temperature bins (1, 1.5 and 2°C of warming), averaged over 19 atmosphere–ocean general circulation models (AOGCMs), at each coral reef grid point included in the comprehensive multi-model Coupled Model Intercomparison Project phase 3 (CMIP3). This is applied for scenarios with 1, 1.5, and 2°C of warming. Data were extracted for each region and for two warming scenarios (+1.5 and +2°C). These values were, respectively, 0.3, 0.6 (Lord Howe), 0.45, 0.7 (Ningaloo), 0.5, 0.7 (Shark Bay), and 0.4, 0.8 (GBR) (Frieler et al., 2013).

To convert values to DHW from DHM, the estimated time to each temperature scenario threshold at $+1.5°C$ and $+2°C$ was calculated based on the moderate IPCC SSP2-4.5 Pathway (Pörtner et al., 2022) as part of the Coupled Model Intercomparison Project phase 5 and 6 of the World Climate Research Programme (CMIP5, CMIP6). For this Intermediate Pathway of greenhouse gas emissions (Pörtner et al., 2022), we calculated the time to reach +1.5 and +2°C, which resulted in estimates of 12 years (2035) and 27 years (2050). Frequency estimates from Frieler et al. (2013) were then converted to cumulative DHMs by multiplying by years to expected warming, and then converted to DHW. An annual rate of change per region per time period was then calculated by solving the equations based on the linear regression model previously described ($-2.9 - (0.2 \times \text{DHW})$). Annual rates of change per species per region per time period (present, 2050, 2100) were modelled and fit according to the estimated degree heating weeks (DHW) experienced at each region per time period. Rates were then applied to estimate the relative abundances calculated per species, resulting in individual abundance trajectories per species. These rates of change were applied to estimate abundances per species, and then normalized to either "1," "0.5," or "0.25" based on methods outlined in Madin et al. (2021) for the subsequent analyses. Relative abundances were used to have a standardized metric between reef regions given absolute abundances of species varied. Further, given we use coral cover as a metric of change (reported in units of relative abundance), this added additional justification to the use of relative compared to absolute abundances.

To predict potential losses of species, we calculated the likelihood of species persistence. We define loss of species as the change in relative abundance of a species at a reef region over time from greater than zero to zero. The ecological persistence metric was calculated using these updated local species-level abundances plus range size and bleaching susceptibility. The relationship between these traits was then fit to ordination space, as developed in Madin et al. (2021). This metric incorporates, per species, a number of factors known to influence ecological persistence; including geographic range size and ecological abundances (e.g., increased range size and abundances decrease the likelihood of extinction), and bleaching susceptibility, in this case, normalized tolerance to heat (e.g., high resistance to thermal bleaching). Briefly, it is estimated by multiplying per species

distances in trait space in an iterative process such that likelihoods of persistence are calculated each iteration. If a species has a greater standardized score of persistence based on the factors listed above, it is less likely to be removed with each subsequent iteration. Trait space was calculated as per methods outlined above and within the studies of Madin et al. (2021) and McWilliam et al. (2018). The calculation of standardized relative percent change in trait space volume between the different climate warming scenarios measures how different two numbers are compared to their average using the following calculation (abs((value1 − value2)/((value1 + value2)/2)) × 100). The higher the percent difference, the more different the values are from each other. By comparing the difference between the values to their average, this approach provides a sense of how significant the difference is relative to the scale of the values themselves. This helps contextualize the percent difference.

2.3 | The impact of relative abundance data on trait space

Given the difficulty in identifying corals to the species level during surveys, we tested the impact of relative abundance estimates per species on the resulting persistence metric and ultimately, functional analysis outputs. To do this, we used a test set of data collected from the whole GBR (Kuo, 2017) and compared this to a dataset collected only from the central GBR by the same team (Baird et al., 2020; Kuo et al., 2023). When only central GBR abundances were used, compared to GBR-wide data, the relative abundances of each species varied (Figure S5). However, we found little difference in resulting trait space in the three functional categories even considering the lower diversity from only including 1/3 of the full GBR range when comparing across present day (Figure S6). Therefore, given both metrics were considered as approaches in calculating relative persistence and trait space, and we found similar results, we can conclude that the relative abundance data were not a main driver of differences in functional trait space results.

2.4 | Current and future climatology

Continent-wide sea surface temperature data were sourced from Bio-ORACLE (Assis et al., 2018; Bosch et al., 2018; Tyberghein et al., 2012) to characterize the different current and future sea surface temperature conditions across the four WH reef regions. This database uses global-scale GIS rasters with a spatial resolution of 5 arcmin (~9.2 km at the equator). The "present day" time period from Bio-ORACLE corresponds with estimates of long-term mean between 2000 and 2014. Temperature forecasting uses the most recent Representative Concentration Pathways to model ecological effects of future climate change scenarios from RCP4.5 for present and future conditions (2050, 2100) (Assis et al., 2018; Bosch et al., 2018; Tyberghein et al., 2012). Specifically, the temperature data that were extracted from the marine Bio-ORACLE dataset layer

was "BO_sstmean." This data layer consists of mean monthly sea surface temperatures. Maps were generated using the R packages *sdmpredictors*, *rgdal*, *maps*, *ggspatial*, *rnaturalearthdata*, *ggplot2*, *stars*, *sf*, and *raster* (Bivand et al., 2015; Bosch et al., 2017; Dunnington & Thorne, 2020; Hijmans et al., 2013; Pebesma, 2018; Pebesma et al., 2019; South, 2017; Wickham, 2011). Data layers were filtered to the boundaries of each WH region, respectively. To generate summary statistics, regional datasets were filtered to only include pixels within the respective marine park boundaries. Mean monthly maximum (MMM) climatology was derived from National Oceanic and Atmospheric Administrations (NOAA) assessment for each region based on data from 1985 to 2012 (Heron et al., 2014), as per the current Coral Reef Watch calculations. MMM climatology was standardized to geographic extent of each reef region by first filtering all data such that they only included temperatures within the MPA boundary. These values were then averaged by first counting the total number of values in each region and then calculating a normalized mean relative change by dividing the mean relative change by the total count per region.

2.5 | Uncertainty and assumptions

We acknowledge that here we assume that the only disturbance is heat stress related to climate warming. This, unfortunately, is not the only stressor coral reefs face, including pressures from deteriorating water quality (Donovan et al., 2021). Further, given the data available, we were not able to capture spatially and taxonomically divergent patterns and were unable to incorporate other factors that will likely impact likelihoods of species ecological extinction risks. These include key demographic processes like growth and reproduction. We also assume when modelling extinctions that the relationship between change in abundance of corals and DHW is linear (as discussed above). Although this may be overly simplistic, we found no evidence that more complex polynomial relationships explained a significantly greater amount of variation in the data (Figures S3 and S4). Hence, although we define extinction risk here as a linear regression dropping below zero, potentially with more complex methods, this would not equal extinction, and instead we suggest alternative modelling methods are more appropriate.

A single model for mean predicted changes in coral cover was applied to each region specifically to calculate a site-specific value. A single model was used because a vast majority of data available in Australia on the long-term trends in coral cover are only available for the Great Barrier Reef. Little to no information is available for Shark Bay, Lord Howe Island or Ningaloo Reef. To this end, we have chosen to construct our model on the best available data from González-Barrios et al. (2023). However, to explicitly capture the uncertainty of using a single model of mean predicted change in coral cover, we explored a range of coral cover and DHW relationships to see how it would impact on the resulting rates of change estimates for each reef. To do this, we sequentially added available global data to our Australian-only dataset, re-constructed both linear and

non-linear models, re-calculated estimates changes in coral cover per reef and compared those to initial "Australian-only" estimates (Figure S7). Specifically, we sequentially added data from low to increasing severity of coral cover change due to bleaching, including: +10% to 0% change, −10% to −20%, and −30% to −40% (González-Barrios et al., 2023). Australian-only derived estimates sat within these bounds, therefore including this increased spatial diversity should also include underestimates (+10% to 0%) and overestimates of bleaching impacts (−10 to −40%) and would allow us to estimate how the rate of change for our sites may vary within a biologically feasible set of conditions depending on values chosen. Additionally, we also re-ran the models to include all data from all central Indo-Pacific reefs, as well as all reefs globally, to see how our WH reef specific rates of change would vary. For reference, the average rate of coral cover changed from our reference −4.5% estimate changed to: −4.08% (all central Indo-Pacific reef), −13.2% (all reefs globally), −3.2% (+10% to 0% bleaching), −6.54% (−10% to −20% bleaching), and −6.58% (−30% to −40% bleaching) (Figure S8).

Overall, we found very little difference in our estimates if we included all central Indo-Pacific reefs (all sites ~0 absolute difference), whereas using all reefs resulted in vast overestimates in declines, more so at +2°C compared to +1.5°C (Figure S8). When adding in progressively more bleaching-impacted reef sites to construct our rates of change models, we found that for +1.5°C of warming, rates of change estimates were underestimated by an absolute difference of 0 to +1 (e.g., from 5.78% rate of change to a 5.74%) or overestimated by +3 to +5. For +2°C of warming, adding additional reefs overestimated rates of change by an absolute difference of +2 to +16. In summary, given data deficiencies in long-term monitoring data for most Australian reef sites, we do not know the "true" model. However, we conclude from past bleaching histories that estimates likely fall within the +10% to 0% bleaching category (González-Barrios et al., 2023), and hence, the uncertainty falls between +0 to +3, equating to change in coral cover estimates between −4.5% to upward of −6.58% to −7% decreases.

Another feature of our approach that may have influenced extinction risk was variation in data availability across taxa. To overcome this common data limitation issue in corals, we averaged across species or taxa by assigning mean family abundances to species without abundance data, even though species with missing values may be rarer than the average species in a taxon. To quantify this impact on extinction risk, we also ran our models using the minimum abundance of a family rather than the mean on the full Great Barrier Reef dataset. We found that the +2°C scenario was unchanged, but that using the minimum family value resulted in $n = 221$ species remaining compared to $n = 251$ at +1.5°C (Figure S9), with the greatest differences in the builders, followed by cementers and relatively little change to fillers. This means using the minimum family value results in a loss of proportionally greater species (−35% compared to −26.1%) and suggests our initial method underestimates extinction risk by about 8.9%.

Finally, it is also important to note that the frequency of heat stress events sourced from Frieler et al. (2012) are based on

multi-models from CMIP3, whereas the time to reach +1.5°C and +2°C for the DHM to DHW conversion is based on CMIP6. Although the outputs from CMIP3 (Frieler et al., 2012) are older, they have been one of the main data sources for IPCC coral reef prediction estimates (see Klein et al., 2024). However, to investigate how this could impact our rate of change in coral cover estimates, we extracted CMIP3 models (Jebeile & Barberousse, 2021) and compared the time to reach +1.5°C and +2°C in CMIP3 relative to CMIP6 and re-calculated our rates of change per reef region. CMIP3 estimates would have resulted in much worse and more variable rates of change in cover (Figure S10). We have opted to use these most up-to-date climate projections but with estimates from Frieler et al. (2012) for consistency with IPCC. As per recommendations set forth in Klein et al. (2024), model outputs were deposited in Github (see data availability statement).

3 | RESULTS

3.1 | Climate forecasts and projected changes in coral abundances on World Heritage reefs

Mean sea surface temperatures (SST) varied across the four WH reef regions under "present" (long-term mean between 2000 and 2014) and future (2050 and 2100) projections (Figure 1a–d). The relative change between current and future projections of mean SST varied across these four WH reef regions (Figure 1a–d; Figure S11). The largest mean changes between the present dataset and 2050 or 2100 occurred at Shark Bay and Ningaloo in 2100 (+1.29–1.24°C), followed by Shark Bay in 2050 and LHI in 2100 (+1.17–1.12°C), LHI and Ningaloo in 2050 (both +1.06°C), and then in 2050 and 2100 on GBR (+1.02–0.8°C). When standardized to the geographic extent of the MPA boundary (Figure 1a–d, shaded regions in maps insets), LHI measured the greatest relative change in both 2050 and 2100 (0.0416–0.0393°C), followed by Ningaloo and Shark Bay in 2100 (0.00157–0.00139°C) and 2050 (0.0034–0.00126°C), and finally the GBR in 2100 and 2050 (0.0000304–0.0000238°C).

Overall, the mean SST increased at each location by >0.8°C (present to 2050, 0.8–1.17°C) and >1°C by 2100 (1.02–1.29°C). The minimum and maximum range of temperatures was largely consistent across the present day, 2050 and 2100, with slight decreases in the range of temperatures projected for LHI and Ningaloo. This trend was as follows: Shark Bay (°C min: 1.13, °C max: 1.19), LHI (1.05, 1.08), Ningaloo (1.03, 1.1), and the GBR (0.7, 0.9). Important thresholds of +1°C of additional warming were reached in all reefs by 2100: Shark Bay (°C min: 1.26, °C max: 1.3), LHI (1.14, 1.1), Ningaloo (1.22, 1.26), and the GBR (0.94, 1.17). Increases in temperature were greatest between present day and 2050 in contrast to comparisons between 2050 and 2100.

In 2050, 37.8% (117 of 309 Bio-ORACLE pixels/reef) of mean temperatures will exceed their respective mean monthly maximum (MMM) temperatures at reef locations in Shark Bay and 11.1% on the GBR (1246 of 11,216 pixels/reef) (Figure 2a). This then
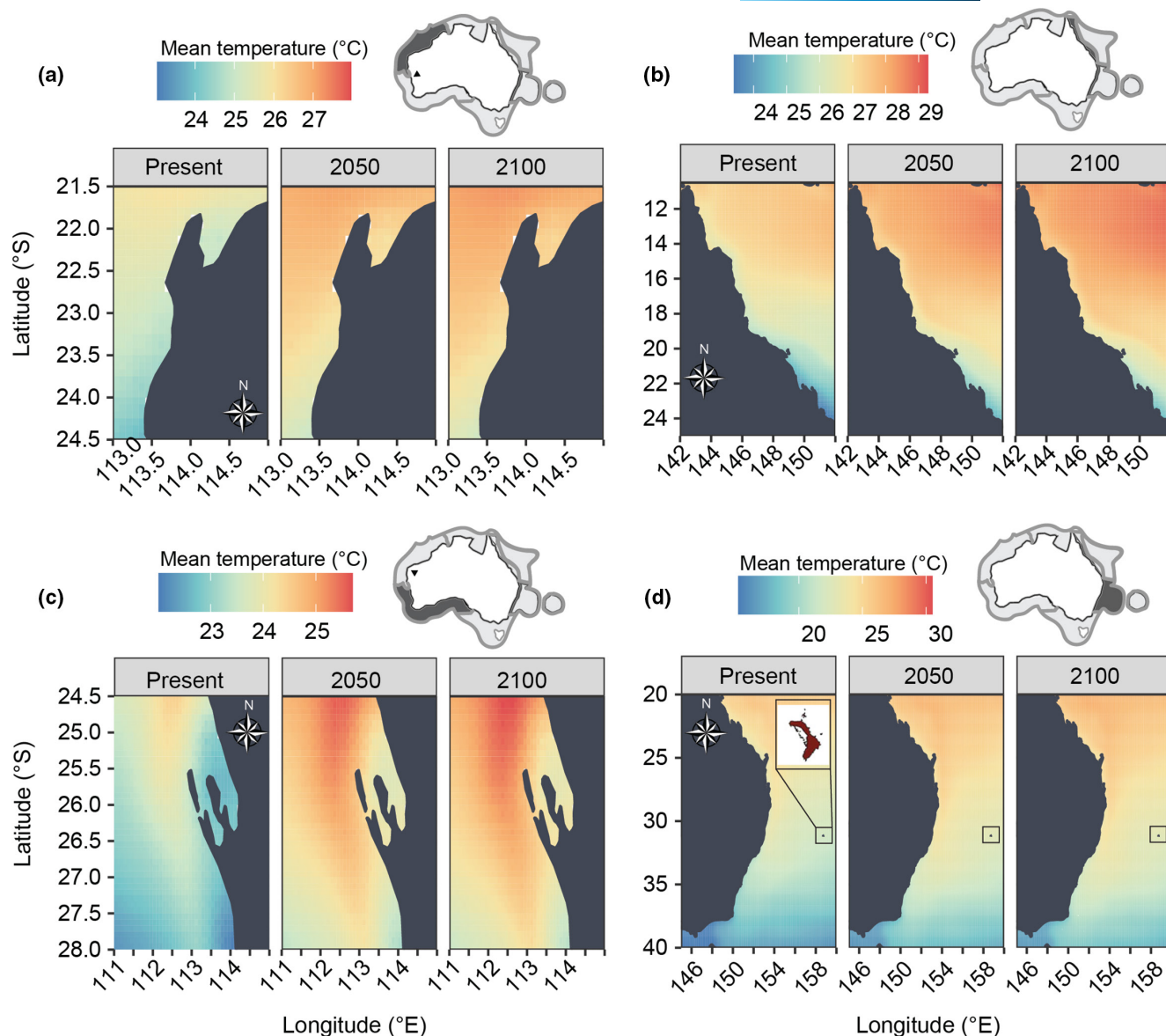
FIGURE 1 Mean sea-surface temperatures are projected to vary across Australia's World Heritage listed reef regions. Colors depict temperatures for "present" (mean long-term mean between 2000 and 2014) and future warming scenarios at +1.5°C (2050) and +2°C (2100) of warming. Projections are sourced from Bio-ORACLE for RCP4.5. (a) Ningaloo Reef, (b) Great Barrier Reef, (c) Shark Bay, and (d) Lord Howe Island. Note the range of colors representing temperature varies per site to emphasize differences between regions. Due to its small size, the location of Lord Howe Island is approximated, and the island has been enlarged for visibility on the map within the inset box. The top right-hand section of each panel shows a map of Australian Parks zoning regions, with the darker grey shading representing the management zone of each reef region of interest. Any map lines delineate study areas and do not necessarily depict accepted national boundaries.

increased to an estimated 45.6% and 26.5% by 2100 (Figure 2b). These trends were not present at LHI or Ningaloo (both 0%) in 2050. In 2100, 4.18% of temperature pixels within Ningaloo will exceed MMM—as temperatures increase from about 1.1°C to >1.2°C (Figure 2b).

Overall, at +1.5°C of warming, modelled relative abundances of species at Shark Bay decreased rapidly, followed by Ningaloo, the GBR and then LHI (Figure 2c). The mean relative abundances across all species per region dropped below 0% at both Ningaloo and Shark Bay. At +2°C of warming, this included the GBR. Given the higher on average relative abundances of many species at LHI, this buffered

declines at +2°C, in which mean abundances are forecast to drop by ~25%.

3.2 | Trait space incorporating ecological resilience

Using outputs from the ecological persistence metric (which incorporated relative abundances, bleaching susceptibility, and range size), functional trait space varied among the four World Heritage reefs (Figure 3a–d, green shading). At present, Ningaloo was most functionally similar to the GBR and Shark Bay (1.4% and 1.6% difference
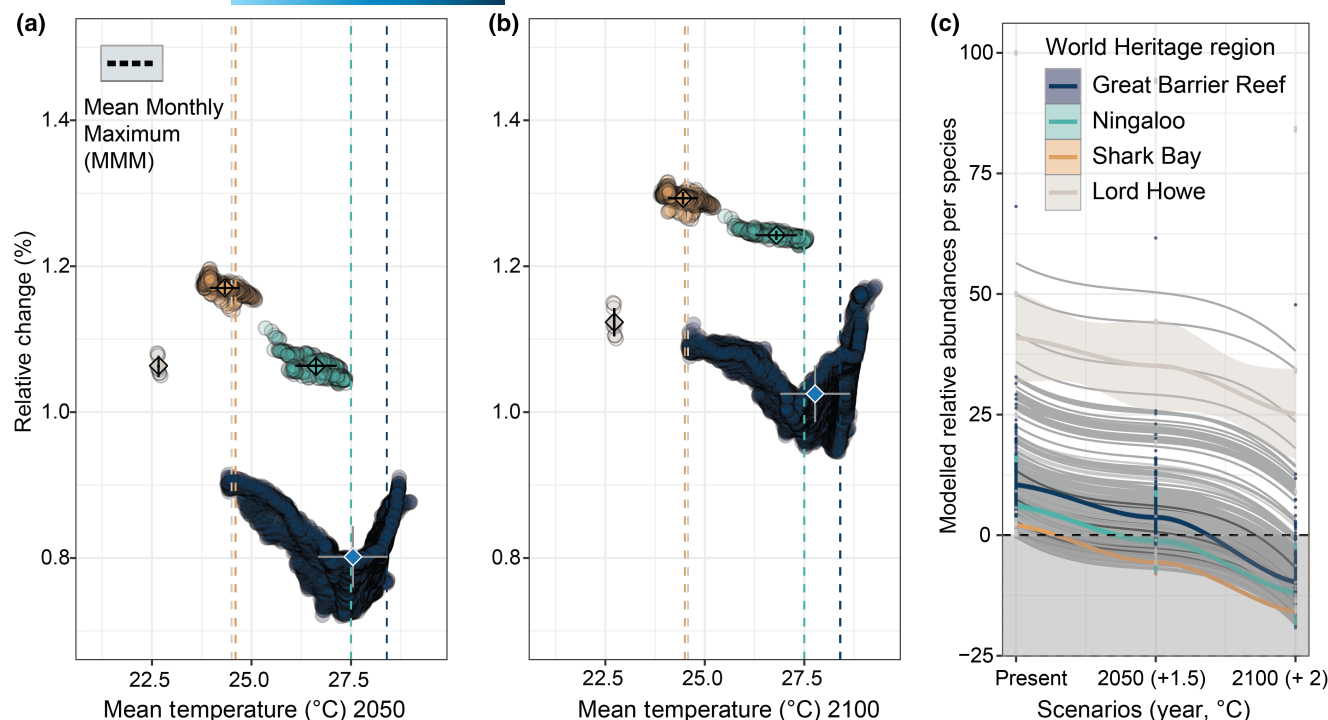
FIGURE 2 Projected environmental change and expected abundance on Australia's World Heritage Reefs. Expected mean temperatures for (a) 2050 and (b) 2100 and relative changes compared to mean present temperatures (%). Expected values were calculated for each Bio-ORACLE pixel within the management boundaries of each WH reef region. Colours represent reef regions (dark blue=Great Barrier Reef (GBR), teal=Ningaloo Reef, Orange=Shark Bay, cream=Lord Howe Island). Vertical dashed lines represent NOAA Coral Reef Watch derived Mean Monthly Maximum (MMM) thresholds for each reef region. Diamonds represent the mean values for each axis, with horizontal standard errors for mean temperatures and vertical standard errors in percentage relative change. The diamond for the GBR has been colored white for visual clarity. (c) Modelled relative abundance for each species at each region shown as an individual grey lines for each temperature scenario. The mean and standard error per region is colored. The dashed horizontal black line at "0" and transparent grey box represents species pushed to extinction, anything below this line represents "extinct" species.

in Principal Component (PC) volume, respectively), whereas LHI was the most distinct compared to the GBR, Ningaloo, and Shark Bay (difference of 23.6%, 22.19%, 20.5%, respectively) (Figure S12). This was also apparent when compared relative to global coral trait space (defined by McWilliam et al., 2018), in which Ningaloo occupied the greatest functional breadth (PC volume), followed by the GBR and Shark Bay, and then LHI (Figure 3a–d). When analysed by genus, the greatest diversity in trait space at present was at Ningaloo, followed by the GBR and Shark Bay and then Lord Howe Island (Figure 3e).
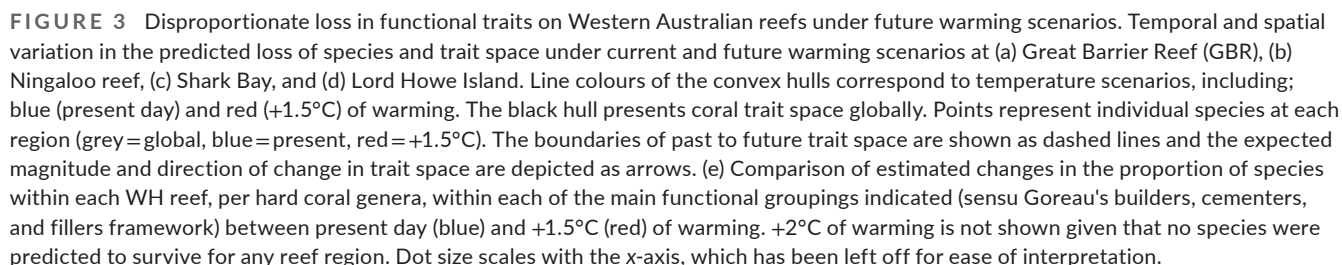
Ecologically, builders made up the greatest proportion of species across all reefs, followed by cementers, and then fillers (Figure 3e). The proportion of species within the fillers category was large (>30) but mostly restricted to one genus (*Acropora*). At Ningaloo, all reef building functions were represented, that is, cementers, fillers and builders were all present. This contrasted to the GBR and Shark Bay, which each had relatively fewer species in the builders category but a greater diversity of cementers. Species assemblages on LHI were underrepresented in both the builders and, to a greater extent, fillers, categories.

At 1.5°C and 2.0°C of warming across the four WH reef regions, the ecological persistence metric predicted a range of species extinctions (Figure 2c, red shading in Figure 3a–d). Of the species with data available to estimate this metric, +1.5°C of warming most severely

impacted Western Australian corals; with projected species losses in the hundreds (species lost: Shark Bay=214, Ningaloo=185). The other reefs regions were less affected (LHI=17, GBR=60).

The numbers of species lost per region was reflected in trait space (Figure 3e). The GBR was projected to lose proportionally fewer species (−26.1%) relative to other reef regions, which corresponded to a −8.8% reduction in trait space volume. This may indicate that reef function was largely unchanged upon comparing present to future assemblages. This loss included mainly species not categorized within the Goreau framework ("NA," −47.3%, data not shown), followed by builders and cementers (−26.7% and −18.6%), then fillers and cementers/fillers (−8.2% and −4.5%). LHI was projected to lose a similar proportion of species (−27.4%) with a relatively smaller reduction in trait space (−3.9%). Relative to present day, LHI reefs lost the greatest proportion of the species overlapping between the cementer/filler category (−75%), followed by builders, and fillers (−35% and −33.3%), cementers (−21.4%) and "NAs" (−6.67%).

Both Ningaloo and Shark Bay are projected to lose a significant proportion of species (62.5% and 96.3%, respectively) with +1.5°C of warming. For Ningaloo, this represents a −52.9% (standardized relative percent change) reduction in trait space relative to the present, including those within a majority of the builder category (−88.9%), cementers and "NAs" (−66.7% and −63.2%), cementers/

FIGURE 3 Disproportionate loss in functional traits on Western Australian reefs under future warming scenarios. Temporal and spatial variation in the predicted loss of species and trait space under current and future warming scenarios at (a) Great Barrier Reef (GBR), (b) Ningaloo reef, (c) Shark Bay, and (d) Lord Howe Island. Line colours of the convex hulls correspond to temperature scenarios, including; blue (present day) and red (+1.5°C) of warming. The black hull presents coral trait space globally. Points represent individual species at each region (grey = global, blue = present, red = +1.5°C). The boundaries of past to future trait space are shown as dashed lines and the expected magnitude and direction of change in trait space are depicted as arrows. (e) Comparison of estimated changes in the proportion of species within each WH reef, per hard coral genera, within each of the main functional groupings indicated (sensu Goreau's builders, cementers, and fillers framework) between present day (blue) and +1.5°C (red) of warming. +2°C of warming is not shown given that no species were predicted to survive for any reef region. Dot size scales with the x-axis, which has been left off for ease of interpretation.

fillers (−46.7%) and fillers (−10.9%). For Shark Bay, +1.5°C resulted in −157.4% decrease in trait space, in which almost all fillers, cementer/fillers, and "NAs" (100%, 100%, 98.0%) were lost. Only a core group of cementers (−84.2%) and one builder species remained (−98.7%). Overall, the number of unique species remaining across the four WH reefs was 275 of the 345 species with available data, representing an overall 20.2% decline in species by 2050. Within this framework, for all WH reef regions, no species were predicted to survive 2°C of warming.

4 | DISCUSSION

Here, we show projected losses of reef function due to ocean warming. Temperature metrics calculated here demonstrate that extreme warming is occurring across all four of Australia's WH reefs, rapidly pushing locations to conditions where significant yearly bleaching can be expected. This aligns with previous climate assessments showing that warming risk along the west coast of Australia is particularly dire at 1–1.5°C, and that by 2°C, all reefs will be under

significant risk of species losses (e.g. reduction in species abundances), local extinctions (total loss of species in that region) and potential collapse (loss of multiple species across multiple functional groups simultaneously) (Frieler et al., 2013; McWilliam et al., 2020; Pratchett et al., 2020). Although these previous assessments were also made across the Australian continent, they were not made per WH reef region. Importantly, we present a detailed and continent-wide assessment that strongly confirms this larger trend. We also show that risks to Indian Ocean reefs were greater in terms of species loss, which translated to greater functional loss in the west compared to the east coast. This extreme loss of function suggests a threshold to resistance may be reached at >1.5°C of warming.

4.1 | Factors influencing extinction risk

Differences in the projections of species loss across the Australian continent may also be partially linked to initial coral assemblage structure among regions (e.g., number of species and overall richness). Overall, some isolated reefs with high environmental uniqueness and

therefore low percentage overlap with other reef regions like LHI retained functions better under warming relative to other isolated reefs like Shark Bay. Other locations with higher initial abundances and many species across large tropical reef-scapes (GBR) also led to greater ecological persistence, resulting in improved functional redundancy and ecosystem stability. One could expect locations with lower diversity to lose proportionally more species (Shark Bay, LHI). However, relative to LHI, Shark Bay fared surprisingly worse, with 96.3% of species lost and the collapse of two out of three functional groups. This finding suggests that initial species pools only partially explain these patterns (Coelho et al., 2023; Gaston, 2000). The complexity of these patterns suggests that multiple factors contributed to functional persistence, not only isolation, species richness, or abundances.

Instead, barriers to dispersal (not analyzed here) may also explain these differences. Where analogous climates exist, species can disperse across patches of habitat that are similar ("stepping-stones," Skeels et al., 2023). In terrestrial environments over evolutionary timescales, the availability of species assemblages and dispersal ability are highly influential in driving colonization rates compared to extinction events (Skeels et al., 2023). Hence, the environment at Shark Bay might lack significant overlap in environmental characteristics with other nearby regions, precluding dispersal, increasing the likelihood of extinction. Further, current biogeographic patterns of species diversity are driven by climatic history, dispersal, and evolutionary history. Therefore, patchiness can lead to either the homogenization or diversification of species boundaries. The environmental uniqueness and connectivity at Shark Bay might therefore better explain the disproportionate decline in species and functional groups under the +1.5°C of warming scenario.

This trend highlights an outstanding question as to whether isolated reefs with fewer species are more susceptible to functional collapse or if this is driven more by ecological differences between species. Historically, isolated locations have generally been expected to have lower diversity. However, it has recently been recognized that geographic extent paired with the uniqueness of climatic conditions better predict biodiversity patterns compared to geographic isolation alone (Coelho et al., 2023). For birds, isolated island locations have been particularly hard hit by extinctions due to their size, climate and isolation (>90% of known extinctions, Cooke et al., 2019). The same is true for mammals (Legge et al., 2023) in conjunction with factors like behavior and the impact from invasive species. Previous paradigms also indicate that higher species richness or greater population sizes should reduce extinction risk (Gaston, 2000) from ecological buffering (i.e., the "replacement" species with similar niches). Taken together and seen in our results, isolation alone or lower diversity does not necessarily result in a greater likelihood of functional collapse (Coelho et al., 2023). Instead, species composition and functional diversity are the driving factors of either persistence or vulnerability.

High-latitude marginal reefs may also be particularly vulnerable to silent extinctions for two reasons. Firstly, high-latitude reefs likely host unique diversity formed under selective pressures driven by unique environmental conditions, reproductive isolation, or that are comprised of isolated populations located at the margins of their environmental tolerance limits. Secondly, in conjunction with the loss of species, warming might also cause changes to colony size distributions on reefs, where there is evidence favoring a shift to fewer, larger colonies (Chong et al., 2023) but that may also result (simultaneously) in a shift to more, smaller colonies. Therefore, the increasing frequency of disturbance events may lead to the loss of very large and very small colonies in the short-term depending on species' life histories. Although it is empirically unclear if these shifts occur after bleaching, more variable marginal reefs have already shifted to fewer larger colonies, which may eventually cause bottlenecks in reproduction and recruitment (Álvarez-Noriega et al., 2018; Chong et al., 2023; Hughes et al., 2019). Overall, there is very little empirical evidence on how bleaching affects size structure and demography and the available evidence is often contradictory. Clearly, more research on the effects of bleaching on demography, in particular variables like growth and fecundity, are required.

WH sites like LHI and Shark Bay, and to some extent Ningaloo, fit these vulnerability criteria (unique conditions with unique biodiversity) and may explain the overall lower abundances of colonies now and into the future. These regions may therefore be predisposed (even before warming) to on average lower relative ecological persistence compared to tropical reefs like the GBR. Persistence is then further eroded by warming. These results again suggest it is not just the richness but that the loss of functional diversity through extinctions that contributes to the loss of functions at marginal reefs. In summary, although we were not able to capture other disturbance events or these key demographic processes such as growth or reproductive potential here, they would surely impact a species' ability to perform reef functions, and therefore their risk of ecological extinction.

Consequently, these functional differences between species may contribute more to extinction risk compared to isolation or lower species abundances. This contrasts with terrestrial species, where migration via dispersal and patterns in abundances drive vertebrates (Skeels et al., 2023) and plants (Yap et al., 2018), and can increase local abundances to offset extinction. As climate warming increases, changes in species relative abundances, not just presence or absence, will be critical to predicting ocean ecosystem responses to climate change (Ehrlén & Morris, 2015). This includes initial abundances pre-disturbance, critical for predicting recovery after marine ecological disturbance (> critical threshold of 66%–75%; Cresswell et al., 2024) and the scale of impact. The prevalence of individual species to naturally fluctuate between positive to negative population growth rates is also important ("living dead populations"; Chong et al., 2023; Dietzel et al., 2020). Interestingly, LHI appears to naturally have lower overall abundances—potentially driven by low "equilibrium local abundances" (Chong et al., 2023; Ehrlén & Morris, 2015). Biophysical modelling in the region suggests dispersal limitation, likely due to currents, between the southern GBR and the Solitary Islands (which lie parallel but inshore to LHI) (Mizerek et al., 2021)—which may result in a migration deficient—where recruitment is

driven more by local settlement compared to dispersal from outside reefs (Harriott & Banks, 1995). Shark Bay is likely to be under similar migration deficient due to currents (Munoz et al., 2023), contributing to lower initial abundances and increased extinction risk. Cleary the magnitude of migration, functional diversity, species assembly and abundances all matter in determining extinction risks.

4.2 | Predictions of species extinctions

Extinctions can have irreversible ecological and evolutionary consequences for ecosystems. Here, by combining functional trait analysis with model estimates of species abundance and persistence, we estimate that at least 70 coral species (~20.2% of the total) will be lost under +1.5°C of warming on these World Heritage reefs. Predictions of extreme species loss reported here are staggering but not unprecedented when compared to estimates of current extinction rates across other taxa. In birds, perhaps one of the best studied organisms, humans are likely responsible for 12% of extinctions (~1300–1500 species, Cooke et al., 2019). Australian mammal extinction rates already exceed global averages (followed closely by other taxa), even relative to other regions of a similarly large size (e.g., North American continent). Australia has also lost disproportionally more mammals (1 in North America compared to 34 in Australia) (Legge et al., 2023).

Although ecologically plausible, extinction rates may be overestimated here for a number of reasons. Corals are notoriously difficult to identify and currently undergoing significant taxonomic revision (Bridge et al., 2023), so it is likely that this has affected abundance estimates for many taxa. This potential bias may then influence calculations of extinction dynamics on reefs. Bleaching tolerance was also empirically derived and likely suffers from methodological biases that may impact our modelled persistence (McLachlan et al., 2021). Hence, this inability to capture likely spatial and taxonomic variabilities suggest that extinction rates could be overestimated. For example, the presented rate of coral cover change exhibits high uncertainty which suggests large spatial variability in trends between surveyed reefs (likely due to a mix of factors including bathymetry, disturbance history and species composition). Applying mean predicted changes in coral cover to an entire region, and across all habitats and depths, and projecting it into the future is therefore likely to overestimate extinction rates as subpopulations might persist for much longer on certain reefs and in certain habitats which act as refugia. Although we found that including non-linear relationships and non-Australian reefs with different bleaching histories did not substantially influence the model rates of change estimated, it still likely has impact on the granularity of results and highlights the paucity of data on most reefs outside the GBR. Future work is needed to resolve these data deficiencies in long-term monitoring of key ecological metrics like coral cover. Regardless, these inferred extinction dynamics use the best available data across this diverse group of species and sheds light on which genera may be lost, which are most vulnerable, and those that are more robust to warming. Importantly,

our projections are also in line with global trends across taxa (Souter et al., 2021). Therefore, given our results across marine taxa and extinction rates across terrestrial Australian ecosystems more broadly (Legge et al., 2023), we conclude that Australia appears to be disproportionally at risk to extinctions globally.

Alternatively, these extinction estimates may also represent an underestimate. The potential for more severe climate change suggests that projected extinctions may turn out to be higher, given the escalating severity of warming. For example, global mean temperatures during the northern summer of 2023 set records every month. June to August were the warmest on record globally, often by a much larger margin than expected given IPCC pathways. The complex interaction between on-going warming from climate change combined with El Niño and other global factors led to hotter than expected seawater temperatures (Hansen et al., 2023). Therefore, Earth's temperatures may surpass modelled estimates sooner than expected. Further, these estimates for SSP2-4.5 only represent the intermediate scenario of multiple projections for different scenarios (Pörtner et al., 2022). Under the five illustrative RCCP scenarios presented, the intermediate SSP2-4.5 scenario predicts exceeding 1.5°C this century, including a likelihood between 2021 and 2040 (Pörtner et al., 2022). Therefore, two other scenarios that include high and very high greenhouse gas emissions scenarios with lower likelihoods, but greater warming, exist (SSP3-7.0 and SSP5-8.5). This warming includes not only predictions of greater absolute temperatures but also the rate of increase (Pörtner et al., 2022).

In this, it is important to highlight the assumptions we have made, including the thresholds set and the uncertainties underlying these thresholds. For consistency with global forecasts for coral reefs, we have chosen internationally recognized IPCC scenarios and sanctioned outputs (Frieler et al., 2012) as sources of input data for these ecological models. However, a recent meta-analysis reports that these outputs, and therefore our assumptions, may be biased upward (Klein et al., 2024), although it is unclear which methods produce "better" estimates without ground truthing projections to empirical data. This again underscores the significant uncertainty in reef futures and the essential nature of robust forecasts for management and conservation action.

Species have likely already been lost in the oceans unknowingly (dark extinctions, Boehm & Cronk, 2021), especially in isolated locations. In other locations where disturbances on reefs have been particularly well documented (Moorea and Jamaica), assemblage structure shifted after disturbance to different species or different traits (McWilliam et al., 2020). This underscores that even with time for recovery and return to coral cover, similar function and diversity did not return. The methods used here could similarly be applied to other global locations to forecast future changes. Indeed, the highest potential for ecological damage occurs at the intersection between both high functional uniqueness and high evolutionary diversity (i.e., a diversity of distinct evolutionary histories) (Skeels et al., 2023). Australia has already declared the first reported extinction attributed to climate change (a mammal, the Bramble Cay Melomys, Hoeppner & Hughes, 2019). Corals,

like many small bodied terrestrial mammals and birds, face similar threats. Such criteria apply to Shark Bay and LHI, as evidenced by smaller overlaps between global traits space and current trait space. Importantly, additional extinctions would prove dire for locations like LHI, where we already predict ~40% of extinctions for known species. Although stark, our results match extremely well with current IPCC estimates (IPCC, 2018) for coral reefs, which predict +1.5°C would result in a 70%–90% loss of corals, and at +2°C, a 99% loss. Indeed, at +2°C, we found that 100% of coral reefs are lost in the absence of acclimation or adaptation. We acknowledge that at least part of this overlap can be due both our work as well as IPCC estimates for reefs relying heavily on assumptions made in Frieler et al. (2012) as explored in Klein et al. (2024). However, our results also align with predictions of decreases in diversity using ancient reef assemblages (Greenstein & Pandolfi, 2008). Hence, we acknowledge that these all may be at risk of overestimation. Although extreme, environmental drivers of change often lead to rapid and dramatic shifts instead of gradual changes (Egidi et al., 2023). Hence, the +2°C of warming projected for 2100 may represent an important tipping point, not just in species loss, but also for loss in ecosystem-wide functions.

4.3 | A focus on whole-ecosystem effects

In this analysis, we identified key reefs of current functional importance and future reefs of vulnerability. At present, functional trait space differs among WH reefs across Australia. Within this continent-wide assessment of trait space, Ningaloo reef and the GBR covered much of the global range of trait availability. Ningaloo was also a national hotspot for species within the builder functional category and the location with the most functionally distinct species (indicated by its higher total overlap with global trait space). It is important to highlight that it isn't only concerning the loss of specific functions like reef building or filing but the loss of trait diversity in general (i.e., the combination of those functions). That is because trait diversity underpins some of the most important ecological functions on reefs, including productivity and reef-building (McWilliam et al., 2020). Comparisons between ancient and modern Ningaloo also show that reef assemblages there have remained relatively unchanged over at least 100,000 years (late Pleistocene; Greenstein & Pandolfi, 2008). This underscores the massive impact that climate warming will have over a relatively short period of time.

Looking into the future, we not only identified the loss of species, but also the loss of whole functional groups. Shark Bay should be of particular concern given the drastic reduction in functional diversity by +1.5°C. Surprisingly, LHI was able to maintain functional diversity even with low species richness and abundances and we found a relative lack of effect on GBR functional space compared to other locations. This could be due to the smaller number of species lost overall or greater potential functional redundancy. This was reflected in the relatively smaller proportional loss in species on the GBR compared

to the disproportionate loss of a number of species of given functions at Ningaloo (builders) and Shark Bay (all categories). Taken together, these results suggest bespoke conservation management is needed across reef regions. International and domestic policies should target areas where both functional and evolutionary histories are at stake.

4.4 | The role of adaptation on reefs

This trait-based approach, by design, incorporates multiple environmental niches simultaneously, where significant differences between trait space suggests the potential for local adaption. Further work incorporating genetic markers would elucidate if this has already occurred and will provide increased accuracy to predictions (Quigley, 2024). These approaches—functional and genetic—are powerful tools to identifying and potentially conserving discrete lineages, species, populations, and functions.

These models do not yet explicitly incorporate increased heat tolerance from adaptation/acclimation or changes in distributions. Indeed, the large-scale differences in temperature patterns across these large temporal and spatial scales will likely be sufficiently large to influence the ecosystem-wide assemblage patterns predicted here and drive local adaption. Even fine scale changes in temperature through processes like heat advection in the oceans can lead to temperature variability on reefs, strongly influencing patterns in local adaption (Quigley & Donelson, 2024). Cleary, adding in adaptative potential will be critical for future management aimed at protecting species against the climate change emergency.

Reefs like Shark Bay and LHI may be at the absolute range margins for many coral species located there. This may represent double-jeopardy for evolutionary potential. The nearly neutral theory of evolution (Ohta, 1973) can provide clues for assessing the potential for selection of traits, like temperature tolerance at the range margins. For example, evidence in salmon suggests that selection is weaker at the range margins due to "surfing" of deleterious mutations, selection efficiency is lower (via greater number of non-adaptive substitutions and lower adaptive substitutions), and effective populations sizes are smaller (Rougemont et al., 2023). Multiple founder events—hallmarks of range margins—also have a similar effect (Rougemont et al., 2023). If adaptation is limited locally, the establishment or maintenance of connectivity and limiting habitat degradation will be critical to counteract extinctions and protect these regions as warming degrades reefs globally.

Evolutionary outcomes will also depend on its genetic isolation. The effects of climate change vary dramatically whether populations are connected or not. The current revision of the "area hypothesis" shows that the total area as well as isolation strongly predict biodiversity, where highly fragmented and isolated areas are generally more biodiverse (Coelho et al., 2023). However, increased gene flow could also lead to decreased speciation and adaptation. For example, projections on outcomes for one coral species (*Porites lobata*) varied from +5% range expansion

to −50% loss, depending on the population structure estimated (Cacciapaglia & van Woesik, 2020). This may be especially true at LHI, where the maintenance of its isolation from coral carrying currents may be blocking gene flow (Harriott & Banks, 1995; Mizerek et al., 2021). Isolation from larval sources that drive genetic isolation at each WH reef will therefore be critical for directing the evolutionary outcomes at these locations. Ultimately, it is not completely known how climate change and isolation will interact to influence evolution on reefs.

Although we incorporated range sizes, a key limitation of this study is that it does not incorporate connectivity (i.e., migration) into regions after species losses. Regions with a high number of colonist species may be important sources of recovery, where the number of potential migration events may increase the probability of ecological persistence. When tested, broader environmental niche space (thereby increasing establishment success probability) and dispersal ability were the greatest predictors in the expansion of geographic footprint of species over long time periods, and not rapid adaptation to new environments (Skeels et al., 2023). Until the taxonomy is resolved, the limits to species boundaries will remain unclear, and may result in less overlap in global distributions, smaller biogeographical ranges and population sizes than initially predicted (Bridge et al., 2023). Interestingly, in these studies, ecology and not adaptation (Siqueira et al., 2022), were the best predictors of species range shifts in the future. Ultimately, the loss of species at major fitness peaks (those that support a wide range of traits) covering many ecosystem services will likely have a disproportionally negative impact on the maintenance of healthy ecosystems.

Of course, species or functions will likely not disappear overnight. Instead, repeated disturbance events will likely result in steady declines in functions over years. Given that a species' ability to perform its ecological functions depends on its abundance and demographic composition (e.g., colony size frequency distributions affect reproductive output and the capacity of a population to provide shelter), functions might decline steadily. Some regions may lose only few species or functions, whilst others may suffer sharp declines. Indeed, the predicted sharp declines in abundances are tantamount to the effective and simultaneous loss of many of these species resulting in rapid functional collapse. Future work should account for these dynamics through the incorporation of long-term monitoring data that include relative abundances or potentially through weighting taxa in trait space.

This work focuses on probable extinctions. However, predicting the success of biological invasions, rates of species extinctions and rescue will all also be needed for a comprehensive assessment of WH persistence. Globally, the source pools, geographic distances between regions, the number of dispersal corridors, dispersal ability, niche breadth across multiple environmental factors (rainfall, temperature rates, and ranges) and species richness drive global biogeographic patterns over ecological and evolutionary timeframes (Skeels et al., 2023). This information, in conjunction with extinction probabilities, have implications for conservation decision-making and action. This is especially true in active management scenarios that require estimates on the movement of organisms based on species boundaries for risk assessments (e.g., Assisted Gene Flow, Quigley, 2024). A functional perspective may provide guidance in these cases. This will also require managers to view protected areas not as "static resources," but as living entities undergoing "ecological and biological process in evolution" (Lin et al., 2023).

5 | CONCLUSION

Understanding the risk of species loss over time is essential information to help policymakers set biodiversity targets (e.g., the IUCN Red List). It is also important for monitoring and protecting remaining species. These predictions identify the winners and losers of functional space on current and future reefs and will be critical for policymakers and stakeholders aiming to achieve the conservation goals pledged in 2022. This first pass at prediction can be subsequently improved and expanded spatially and offers estimates of biodiversity change that are naturally useful at policy-related scales to guide adaptive conservation decisions. Many studies of species extinctions highlight the need to go beyond documenting loss to quantifying debts in functioning (Cooke et al., 2019). We do that here to understand losses to ecosystem functioning on reefs. We also show that the initial source pool is important but not the main driver of ecological persistence and that richness in species pools is critical to driving ultimate long-term resilience in functional assemblage structure. We also show that reefs in the Indian Ocean are under particular risk relative to their east coast counterparts, in agreement with previous global projections (Frieler et al., 2013). Critically, all reefs are at risk at +2°C of warming.

Of course, warming is only one of the environmental pressures impacting reefs locally and globally (Gove et al., 2023). However, this work proactively identifies regions and species most at risk from climate-induced extinction, critical to protection. By delineating species ranges and vulnerabilities, we also provide critical information needed for policy recommendations for applied conservation actions, like the assisted migration of species. This includes the identification of which species are threatened with increased climate extinction risk (Brodie et al., 2021). This study is an important contributor to the field as it provides projections of species-level abundance and ecosystem function—parameters necessary to meet recent landmark global biodiversity goals. Finally, as the world shifts to a nature positive mindset, managers will require information not only on species losses but also on functional gains, to determine how best to bolster ecosystem resilience.

AUTHOR CONTRIBUTIONS

Kate M. Quigley: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; validation; visualization; writing – original draft; writing – review and editing. **Andrew H. Baird:** Conceptualization; data curation; resources; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Zenodo at https://zenodo.org/doi/10.5281/zenodo.12194896. R code is also available via GitHub at https://github.com/LaserKate/Futurefunction_GCB.

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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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