

RESEARCH ARTICLE

Diminishing potential for tropical reefs to function as coral diversity strongholds under climate change conditions

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Abstract

Aim: Forecasting the influence of climate change on coral biodiversity and reef functioning is important for informing policy decisions. Dominance shifts, tropicalization and local extinctions are common responses of climate change, but uncertainty surrounds the reliability of predicted coral community transformations. Here, we use species distribution models (SDMs) to assess changes in suitable coral habitat and associated patterns in biodiversity across Western Australia (WA) under present-day and future climate scenarios (RCP 2.6 and RCP 8.5).

Location: Coral reef systems and communities in WA.

Methods: We developed SDMs with model prediction uncertainty analyses, using specimen-based occurrence records of 188 hermatypic scleractinian coral species and seven variables to estimate present-day and future changes to coral species distribution and biodiversity patterns in WA under climate change conditions.

Results: We found that suitable habitat is predicted to increase across all regions in WA under RCP_{2.6}²⁰⁵⁰, RCP_{8.5}²⁰⁵⁰ and RCP_{2.6}²¹⁰⁰ scenarios with all tropical and subtropical regions remaining coral biodiversity strongholds. Under the extreme RCP_{8.5}²¹⁰⁰ scenario, however, a clear tropicalization trend could be observed with coral species expanding their range to mid-high latitude regions, while a substantial drop in coral species richness was predicted at low latitude tropical coral reefs, such as the inshore Kimberley and offshore NW reefs. Despite the predicted expansion south, we identified a net decline in coral biodiversity across the WA coastline.

Main conclusions: Results from the models predicted higher net coral biodiversity loss at low latitude tropical regions compared with net gains at mid-high latitude regions under RCP_{8.5}²¹⁰⁰. These results are likely to be representative of latitudinal trends across the Southern Hemisphere and highlight that increases in habitat suitability at higher latitudes may not lead to equivalent biodiversity benefits. Urgent action is needed to limit climate change to prevent spatial erosion of tropical coral communities, extinction events and loss of tropical ecosystem services.

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KEYWORDS

biodiversity, coral reef, global change ecology, refugia, Scleractinia, transformation, tropicalization, Western Australia

1 | INTRODUCTION

Global climate change poses a major threat to terrestrial and marine ecosystems (Burrows et al., 2011). Losses or major shifts in the distribution of habitat-forming taxa have led to cascading impacts on biodiversity, lowered productivity and impaired ecosystem functioning (Chen et al., 2011; Hoffmann et al., 2019; Sorte et al., 2010). Even though variable responses to climate change have been reported across different taxa (Chen et al., 2011), it has been estimated that climate-induced range shifts occur faster in marine environments than in terrestrial environments (Sorte et al., 2010). This could be related to the capacity of marine organisms to disperse far distances (Kinlan & Gaines, 2003), and a lag in the response of terrestrial organisms to temperature isotherm shifts (Chen et al., 2011; Lenoir et al., 2019). Habitat transformations, range contractions and extensions of marine habitat-forming taxa such as macroalgae (Vergés et al., 2019), mangroves (Saintilan et al., 2014), seagrass meadows (Hyndes et al., 2016) and coral reefs (Tuckett et al., 2017; Yamano et al., 2011) have already been documented around the world, resulting in the emergence of novel ecosystem configurations (Graham, Cinner, et al., 2014; Pinsky et al., 2020; Vergés et al., 2014). Specifically for coral reefs, climate change-induced coral bleaching leads to coral reef degradation and various other ecological changes including dominance shifts, local extinctions, tropicalization (Greenstein & Pandolfi, 2008; Hughes et al., 2018; Muir et al., 2015; Sorte et al., 2010; Thomson, 2010; Wernberg et al., 2016) and changes to species interactions (Vergés et al., 2014). Other studies have predicted that under climate change, habitat suitable for corals will contract; and that brooding species may replace spawning species as the dominant taxa in depleted recruitment pools (Hughes et al., 2019) or that small or isolated populations may become locally extinct (Richards & Day, 2018; Thomas et al., 2017). Long-term coral cover monitoring data have shown that the majority of coral reef systems in Western Australia (WA) have been impacted by reoccurring mass bleaching events and cyclone activity over the last decade, resulting in drastic reductions in coral cover and changes in coral community composition (Depczynski et al., 2013; Gilmour et al., 2019; Moore et al., 2012; Speed et al., 2013). Such declines in the health, extent or functionality of coral communities can have cascading effects for the wider reef ecosystem (Kubicek & Reuter, 2016), and an understanding of how ecological changes may manifest on coral reefs in the future is essential to maximize the ecological opportunities that exist for safeguarding diversity.

Species distribution modelling (SDM) enables changes in species environmental and habitat area to be predicted over time and space (Elith & Leathwick, 2009; Freeman et al., 2013). These models have been used extensively to model the current distribution of terrestrial and marine organisms, however, only a limited number of

marine species distribution studies have implemented SDMs to predict distributional changes of marine invertebrate species under climate change conditions (Cheung et al., 2009; Robinson et al., 2011, 2017). Notwithstanding studies focussing on cold water coral species (Bridge et al., 2012; Davies & Guinotte, 2011), soft corals (Bridge et al., 2012; Done, 1982; Veron, 2000; Yesson et al., 2012), Hawaiian (Franklin et al., 2013; Robinson et al., 2017) and the Atlantic communities (Rodríguez et al., 2019), limited number of SDM studies have predicted changes in scleractinian coral biodiversity in the Indo-Pacific under future climate scenarios (Cacciapaglia & van Woesik, 2015, 2016, 2018; Descombes et al., 2015). Furthermore, few studies addressed the uncertainty of suitable habitat predictions in SDMs based on the variability in environmental input data (Braunisch et al., 2013) and the use of environmental variables across different temporal scales (Pennino et al., 2019). Indeed, Braunisch et al. (2013) showed that SDMs with similar goodness of fit but with different sets of correlated variables could have varying, even generating opposite predictions within and between future climate scenarios.

Spanning more than 20,000 km of coastline, 25° of latitude and a sea surface temperature range of more than 12°C (Saha et al., 2018; see Figure S1 and supplementary text for more information on the reef systems in the study area), WA provides the ideal model system to test hypotheses about the configuration of future reefs under climate change conditions. Here, we compile all available scleractinian coral species occurrence records from the Western Australian Museum and Queensland Museum and apply SDMs to estimate the present-day and future extent of suitable coral habitat and changes to species richness under two future climate scenarios (RCP 2.6 and RCP 8.5) in 2040–2050 and 2090–2100. We examine whether present-day biodiversity hotspots are likely to provide consistent levels of high coral biodiversity over time, that is future strongholds for coral biodiversity under climate change conditions. We also investigate whether certain reproductive or life history modes of corals are predicted to support greater survivability under future environmental conditions. Finally, to evaluate the confidence in model performance and its predictions, we apply a model projection uncertainty analysis that involves refitting the SDMs of all modelled species with variables that represent the temporal variance in environmental predictor data.

2 | METHODS

2.1 | Coral species occurrence data

Specimen-based scleractinian coral occurrence records were obtained from the WA Museum and Queensland Museum in September

2018. Quality control procedures were applied to all occurrence data, which included the removal of taxonomically undefined or higher-level taxonomic records, mesophotic and deep-sea coral records (>40 m), records outside Australia's Exclusive Economic Zone (EEZ) and duplicate records (see Figure S1). Furthermore, all species records were updated to align with the current classification in the World Register of Marine Species (as of January 2019) and all species were grouped as either tropical (species within 10°S to 27.2°S), tropical-subtropical (27.2°S to 31.5°S) and tropical, subtropical and temperate (31.5°S to 36°S).

2.2 | Environmental and geomorphological variables

Environmental and geomorphological variables were used in SDMs as predictors of species' suitable habitat under present-day and future climate scenarios. Present-day suitable habitat patterns were estimated based on variables that directly influence coral growth, persistence and settlement success (Maina et al., 2011) that include sea surface temperature (SST), temperature anomalies, water column optical properties and geomorphological variables (see Table 1).

Future SSTmax and SSTrange were estimated from the average of the CCSM4, HadGEM2-ES and MIROC5 models (Assis et al., 2018). These three Atmosphere-Ocean General Circulation Models (AOGCMs) represent the variability in tropical SST projections of AOGCMs in the CMIP 5 multimodel ensemble database (see Table S1; Mizuta et al., 2014; Taylor et al., 2012). Data from two Representative Concentration Pathway (RCP) scenarios, RCP 2.6 ("best case") and RCP 8.5 ("high emissions") were used. RCP 2.6 and RCP 8.5 SST data were resampled to 4 km spatial resolution with the NASA/OB.DAAC Data Analysis Software (NASA Ocean Biology Processing Group, 2019). Projected annual SST data from the three AOGCMs between 2040–2050 and 2090–2100 were averaged to obtain the future mean SSTmax and mean SSTrange under RCP 2.6 and RCP 8.5 climate scenarios (see Figure S2; Assis et al., 2018). We refer to these climate scenarios at 2050 and 2100 as $RCP_{2.6}^{2050}$, $RCP_{8.5}^{2050}$, $RCP_{2.6}^{2100}$ and $RCP_{8.5}^{2100}$, respectively.

Kriging interpolation (Assis et al., 2018; Zhou & Zhang, 2014) followed by nearest neighbour resampling (Gogina & Zettler, 2010; Golicher et al., 2012; Jones & Cheung, 2015) was applied to all raster data to match the 250 m bathymetry grid of Australia (Whiteway, 2009). All variables were then clipped to the 40 m depth isobath that represents the depth limit where most photic, reef building and hard scleractinian corals are found along the WA coastline and offshore reefs.

To minimize overfitting, variables that had an absolute Pearson correlation <.85 and also had future prediction data available for 2040–2050 and 2090–2100 were selected for SDMs (Elith et al., 2006). For instance, variable thermal stress anomalies (TSA) were excluded due to its high negative correlation with SSTrange ($r = -.90$, p -value < .001) and the fact that future TSA layers are not available. The resultant variables (see Table 1) have also been shown to be fundamental in coral growth (Maina et al., 2011).

2.3 | Model fitting, variable selection and parsimonious model evaluation

In order to estimate the present-day and future suitable coral habitat along the WA coastline, we used the maximum entropy (MaxEnt) algorithm in the "dismo" R package (Hijmans et al., 2017). MaxEnt is one of the most common modelling approaches for SDMs and was chosen due to its ability to handle presence-only data (Elith et al., 2006, 2011; Phillips & Dudik, 2008). To avoid overprediction, only species with ≥ 10 spatially unique records were included (Wisn et al., 2008). Although the model predictions can be influenced by sampling bias and spatial autocorrelation of the occurrence records (Moran I correlation test, p -value < .001; Kramer-Schadt et al., 2013), all records were integrated into the models due to the low number of unique occurrence records within each coral species. This resulted in a total of 6,440 records across 205 coral species to be retained for model integration (see Figure S1).

Prior to constructing the present-day and future coral suitable habitat, models were fitted and evaluated for these 205 species using background spatial point customization (Merow et al., 2013), data splitting into train/test datasets (Araújo et al., 2005) and variable selection to construct the most parsimonious model (Austin & Van Niel, 2011). For each species modelled, 1,000 background spatial points were randomly selected across the study area, bounded by the Australian EEZ depth of ≤ 40 m. Before the background points were generated, a 9 km-radius mask around known locations was applied to exclude background points close to the occurrence locations and avoid variable replication. A radius of 9 km was used based on the coarsest resolution of raw environmental and geomorphological variable data.

Model performance for each species was evaluated with an independent test dataset, where the occurrence and background data were partitioned 75/25 into training/testing datasets (Araújo et al., 2005; Hastie et al., 2009; Merow et al., 2014; Vignali et al., 2020). Five replicate models were constructed on the training dataset with default model features and regularization settings, configured to select the highest contributing variables for the most parsimonious model (Elith et al., 2011). Average variable permutation importance across the five model replicates was used to exclude variables with a permutation importance $\leq 1\%$ in the most parsimonious model (Li et al., 2020; Sobek-Swant et al., 2012; Williams et al., 2012). The threshold independent and dependent metrics, area under the curve (AUC; Beaumont et al., 2019) and sensitivity were used to evaluate model performance on the withheld test data. Parsimonious SDMs with AUC test > 0.7 were retained to spatially estimate the present-day suitable habitat and to project it to future climate scenarios (Moraitis et al., 2019). A small number of species that had optimal models (AUC > 0.7) but with a sensitivity score of zero were removed from this study to improve the accuracy of downstream model projection analyses. Furthermore, model performance metrics, specificity, maximum kappa and total skill statistic were calculated on the retained parsimonious models (see Table S2; Franco et al., 2018; Martínez et al., 2018).

TABLE 1 Environmental and geomorphological variables considered for coral species distribution modelling grouped in sea surface temperature, temperature anomalies, water column optical properties and geomorphological variables

Class	Variables	Units	Spatial Resolution (km ²)	Temporal Resolution	Temporal intervals	Raw temporal data	Source	Sensor
Sea surface temperature (SST)	Mean SST	Kelvin ^a	4.16	1982–2017	Weekly	Weekly	CorTad version 6 ^a	AVHRR
	Mean SSTmin	Kelvin	4.16	1982–2017	Annual	Monthly	CorTad version 6	AVHRR
	Mean SSTmax (*)	Kelvin	4.16	1982–2017	Annual	Monthly	CorTad version 6	AVHRR
	Mean SSTrange (*)	Kelvin	4.16	1982–2017	Annual	Monthly	CorTad version 6	AVHRR
	Mean SST standard deviation	Kelvin	4.16	1982–2017	Weekly	Weekly	CorTad version 6	AVHRR
Temperature anomalies	Mean thermal stress anomalies (TSA)	Kelvin	4.16	1982–2017	Annual	Weekly	CorTad version 6	AVHRR
	Mean sea surface temperature anomalies (SSTA) (*)	Kelvin	4.99	1985–2017	Annual	Annual	Coral Reef Watch ^b	AVHRR
Optical	Mean Chlorophyll a (Chl a ^c)	mg/m ³	4	2002–2012	Monthly	Monthly	Globcolour ^d	Meris, modis, viirs and seawifs
	Mean total suspended matter (TSM) (*)	g/m ²	4	2002–2012	Monthly	Monthly	Globcolour	Meris
	Mean light intensity at max depth (*)	einstein/m ² /day	9.2	2002–2014	Monthly	Monthly	Bio Oracle version 2 ^e	Derived from Globcolour data
Geomorphological Variables	Bathymetry (*)	meter	0.25	2009	—	—	Geoscience Australia ^f	Multibeam
	Terrain roughness (rugosity) (*)	degrees	0.25	2009	—	—	derived from bathymetry	—

Note: (*) represent “less correlated variables” used to incorporate in the SDMs.
^aValues in Kelvin where transformed to °C (Saha et al., 2018).
^bLiu et al. (2018).
^cChlorophyll a in case 2 waters—waters where phytoplankton concentration is lower than inorganic particles (coastal waters).
^dGlobcolour data (<http://globcolour.info>) used in this study has been developed, validated and distributed by ACRI-ST, France.
^eAssis et al. (2018).
^fWhiteway (2009).

2.4 | Estimating uncertainty in present-day and future suitable habitat and species richness

In SDMs, the temporal variability within environmental variables is often overlooked when assessing the precision of model performance and prediction outcomes. We incorporate both spatial and temporal variance allowing a more complete representation of the environmental variables in the SDMs, whereby the temporal variance acts to inform the precision of the suitable habitat and species richness predictions. Here, a two-tailed 95% confidence interval around the means of SSTmax, SSTrange, TSM and SSTA (for present-day conditions), as well as for SSTmax and SSTrange (for future conditions), was constructed to represent the temporal variability (see example plots of interannual variability in SSTmax and SSTrange in Figure S3). All 205 species were remodelled separately with the lower-bound and upper-bound confidence interval variable data. The most parsimonious SDMs used for suitable habitat and species richness predictions were chosen by applying the same model selection parameters used in the models constructed with mean variable data. SDMs constructed using the mean and 95% confidence interval variable values, hereafter referred to as the mean (M), lower-bound (LB) and upper-bound (UB) model types, were statistically evaluated on the model performance, variable importance ranking (as well as comparing the frequency of best explanatory variables across the model types; see Table S3), predicted suitable habitat and species richness between model types. The statistical evaluation of the models used in this uncertainty analysis followed Braunisch et al. (2013) and Bucklin et al. (2015) (see supplementary text for further details).

2.5 | Model predictions

Species with parsimonious models that passed AUC and sensitivity model performance thresholds across the LB, M and UB model types and that had SST variables selected as explanatory variables for all three model types were retained for model projections analysis. In total, 188 species passed the selection criteria for all model types (~61% with AUC > 0.9; see Table S2) and were thus used to estimate the suitable coral habitat and biodiversity hotspots under the present-day and four future climate conditions (RCP_{2.6}²⁰⁵⁰, RCP_{2.6}²¹⁰⁰, RCP_{8.5}²⁰⁵⁰ and RCP_{8.5}²¹⁰⁰) across the WA coastline and the following nine regional zones: Cocos (Keeling) Islands, Christmas Island, offshore reefs on the north-west (NW) shelf, inshore Kimberley, Dampier-Pilbara, Ningaloo-Exmouth Gulf, Shark Bay, Houtman Abrolhos Islands and the south coast area of WA. For every species, continuous habitat suitability predictions were converted into binary values (occurrence [1] and absence [0]) using the maximum sensitivity and specificity threshold (Liu et al., 2013). Total area of occurrences was converted to km² to determine the present-day and future suitable habitat. Shifts in suitable habitat were estimated by overlaying the future binary habitat suitability predictions with present-day binary predictions using package “biomod2” (Thuiller et al., 2009).

To evaluate spatial shifts in suitable habitat at community level, we characterized species richness as the number of species predicted to be present in the binary habitat suitability predictions across all modelled species (Distler et al., 2015; Schmitt et al., 2017; Zellmer et al., 2019). Areas with high predicted species richness could then be considered as biodiversity hotspots and strongholds under present-day and future climate conditions, respectively. To evaluate shifts in biodiversity strongholds across the M, LB and UB model types under present-day, RCP_{2.6}²¹⁰⁰ and RCP_{8.5}²¹⁰⁰ climate conditions, we visualized the standard deviation of the total species richness across the three model types (Senay & Worner, 2019). Predicted mean suitable habitat and species richness were presented separately in regard to the mean model type followed by the percentage relative range across the three model types calculated as (highest – lowest)/(mean across all model types) × 100%.

Finally, coral species were classified according to range extent (tropical, tropical/subtropical, tropical/subtropical/temperate), life history (competitive, competitive/generalist, generalist, stress-tolerant, weedy and others) and reproduction mode (broadcast, brooding; Darling et al., 2012; Graham, Chong-Seng, et al., 2014; Richmond & Hunter, 1990; Zinke et al., 2018) to compare predicted future suitable coral habitat between classification groups. All analyses were conducted in ArcGIS version 10.3 (ESRI, 2011), Climate Data Operator (Schulzweida et al., 2006) and R version 3.6 (Rstudio & Team, 2015).

3 | RESULTS

3.1 | Present-day coral distribution range and future suitable habitat changes along the WA coastline

Significant differences in future suitable habitat patterns were observed under RCP 2.6 and 8.5 climate scenarios ($\chi^2 = 173.77$, p -values < .001; see Table S4 for post hoc analysis) across WA and regional areas (Kruskal, p -values < .001), except for Cocos (Keeling) Islands ($\chi^2 = 2.61$, p -value = .62; see Table S4). Under present-day conditions, the predicted suitable habitat along the WA coastline overlapped with known high coral biodiversity regions such as the offshore reefs and the inshore Kimberley. Ningaloo-Exmouth Gulf, Shark Bay and the Houtman Abrolhos Islands were also identified as additional potential biodiversity hotspots, hosting between 50% and 98% of the 188 modelled coral species (see Figures 1 and S4). Under RCP 2.6, suitable habitat across the WA coastline was predicted to expand in both southerly (between 20 and 35 °S) and northerly (between 13 and 18 °S) directions from 15,615 km² ± 7.88% (present-day) to 36,119 km² ± 11.03% (2050) and 36,598 km² ± 17% (2100), respectively (see Figures 1 and 2; Table S4).

Increases in suitable habitat were predicted under RCP_{2.6}²¹⁰⁰ when compared to present-day conditions (see Figures 2 and S4, Table S4), particularly in the inshore Kimberley region (8,251 km² ± 8.76% to 15,966 km² ± 22.48%), Dampier-Pilbara region (2,421 km² ± 14.34% to 11,526 km² ± 1.86%), Ningaloo-Exmouth Gulf area (1,319 km² ± 8.46%

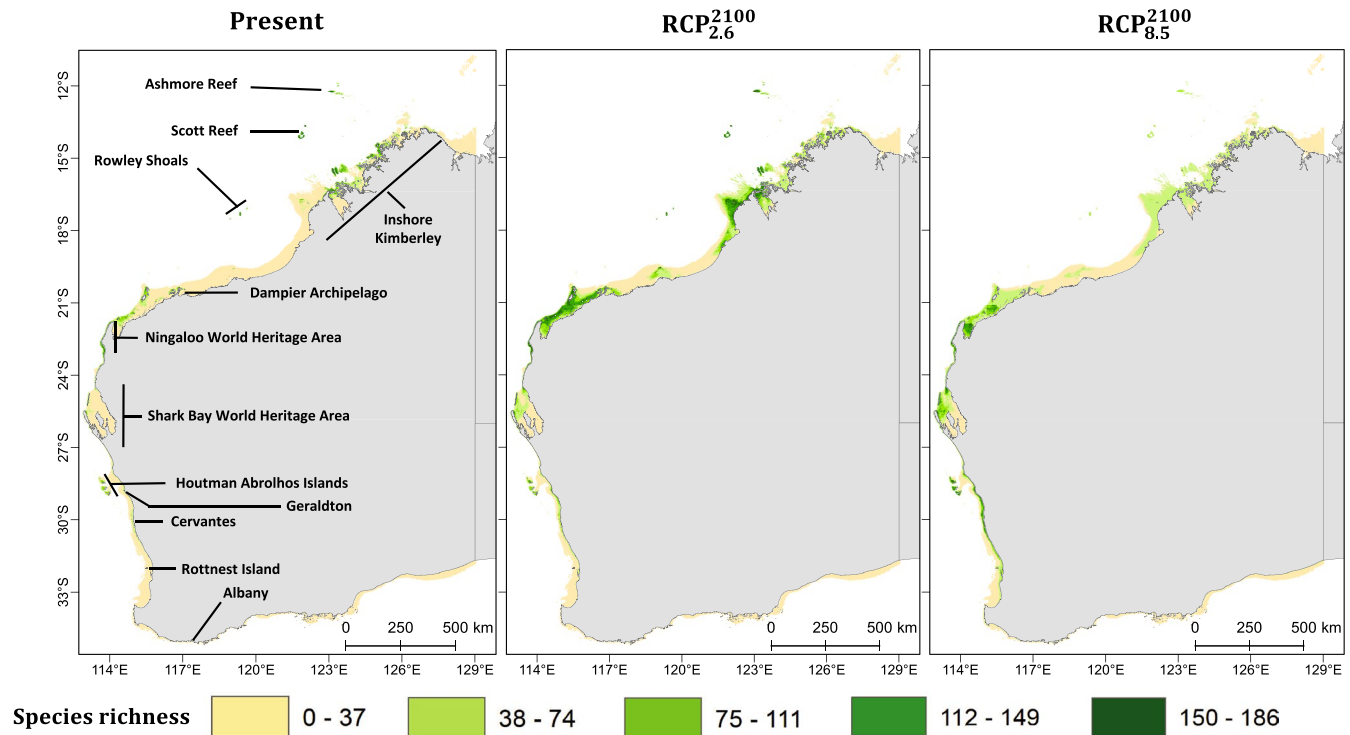


FIGURE 1 Predicted coral species richness in WA based on habitat suitability using mean-type model data under present-day and future climate conditions—RCP 2.6 (best case) and RCP 8.5 (extreme case) scenario in 2090–2100

to $2,733 \text{ km}^2 \pm 13.95\%$ and Shark Bay ($809 \text{ km}^2 \pm 14.36\%$ to $2,121 \text{ km}^2 \pm 22.53\%$). Under $\text{RCP}_{8.5}^{2050}$ and $\text{RCP}_{8.5}^{2100}$, an increase in temperature was estimated to drive contractions in coral suitable habitat, especially at lower latitudes (see Figures 1 and 2, Table S4). For instance, known coral biodiversity hotspots such as the offshore reefs on the NW shelf were predicted to decrease in suitable habitat from $635 \text{ km}^2 \pm 1.89\%$ to $310 \text{ km}^2 \pm 5.61\%$ under $\text{RCP}_{8.5}^{2100}$. After accounting for zero inflation by a $\log(x + 1)$ transform, an average decline of 34.01% in habitat suitability was predicted in the inshore Kimberley region under $\text{RCP}_{8.5}^{2100}$ (see Figure 2), whereas under the extreme $\text{RCP}_{8.5}^{2100}$ scenario, the overall suitable habitat along the WA coastline increased from $15,615 \text{ km}^2 \pm 7.87\%$ to $31,688 \text{ km}^2 \pm 11.40\%$. This increase was driven by habitat gains in mid-high latitude regions including Shark Bay ($809 \text{ km}^2 \pm 14.36\%$ to $3,264 \text{ km}^2 \pm 19.84\%$), the Houtman Abrolhos Islands ($396 \text{ km}^2 \pm 5.79\%$ to $748 \text{ km}^2 \pm 7.25\%$) and the south coast of WA ($587 \text{ km}^2 \pm 11.64\%$ to $2,120 \text{ km}^2 \pm 0.75\%$; see Figure 2 and Table S4).

3.2 | Predicted species richness and potential future biodiversity hotspots along the WA coastline

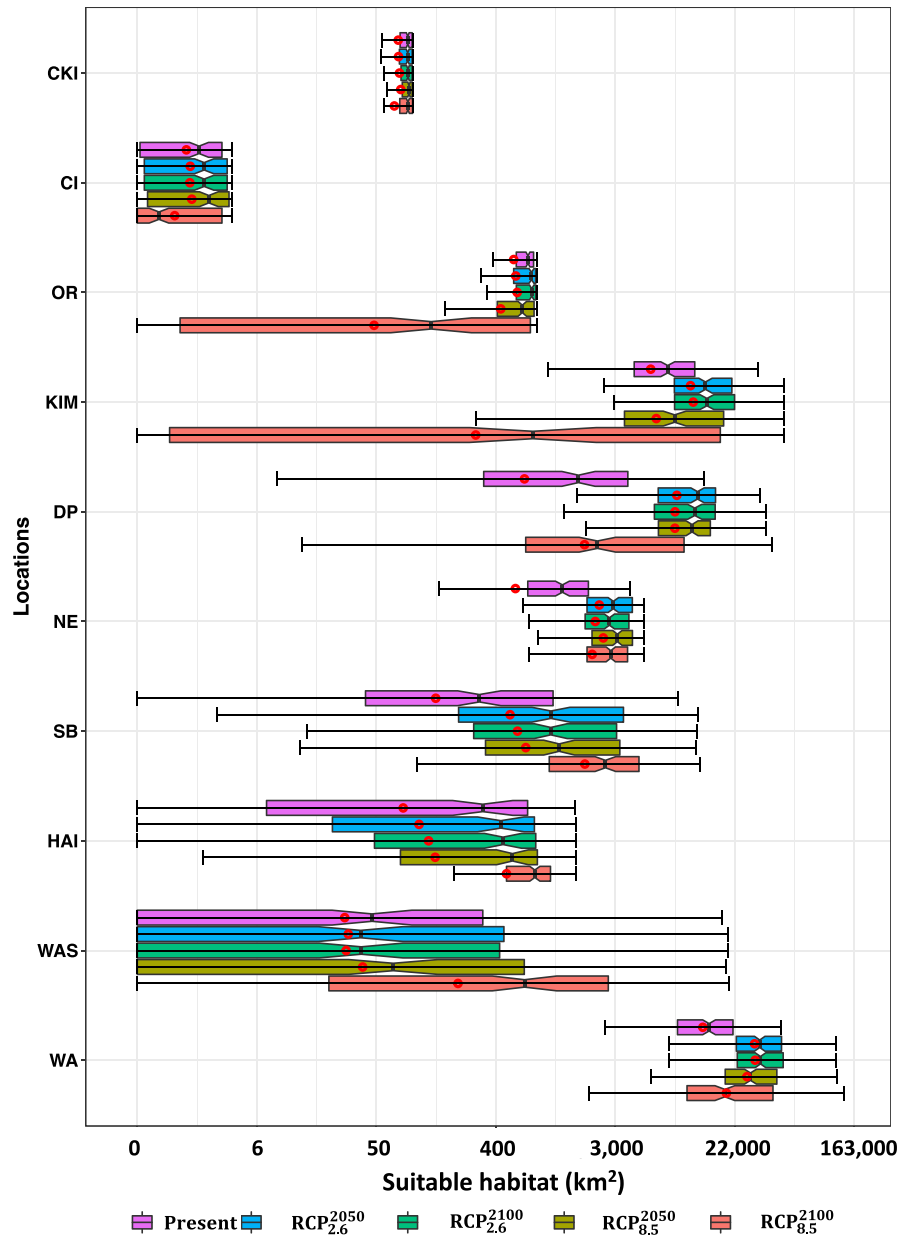
Differences in predicted species richness were significant along the whole WA coastline and some regions for the mean-type SDMs between present-day and the four future climate conditions (Kruskal, p -values $< .001$; see Table S4 for post hoc analysis), except for the Cocos (Keeling) Islands, Christmas Island, offshore reefs on the NW

shelf and Dampier–Pilbara region. Species richness along the WA coastline was estimated to increase under $\text{RCP}_{2.6}^{2100}$ from present-day conditions ($19 \pm 5.4\%$ species to $44 \pm 11.5\%$ species; see Figures 1 and 3, Table S4). Regionally, species richness was estimated to roughly double across all regions, especially at the Dampier–Pilbara ($10 \pm 20\%$ species to $49 \pm 2.1\%$ species) and Ningaloo–Exmouth Gulf regions ($51 \pm 8.1\%$ species to $107 \pm 14.2\%$ species; see Figure 3, Table S4). Changes in biodiversity followed the shift in suitable habitat described above, where species richness was predicted to decrease under $\text{RCP}_{8.5}^{2100}$ from present-day conditions, especially at Christmas Island ($85 \pm 4.6\%$ species to $66 \pm 4.4\%$ species) and offshore reefs on the NW shelf ($149 \pm 2.0\%$ species to $72 \pm 5.4\%$ species; see Figure 3, Table S4). In contrast, mid-latitude regions were estimated to increase substantially in coral species richness under $\text{RCP}_{8.5}^{2100}$ from present-day conditions, for example Shark Bay ($12 \pm 8.6\%$ species to $48 \pm 20.2\%$ species) and the Houtman Abrolhos Islands ($49 \pm 6.2\%$ species to $92 \pm 7.5\%$ species; see Figure 3 and Table S4).

3.3 | Future environmental niche area prediction across range extent, reproductive mode, life history and genera categories

When grouping the 188 species according to their range extent, differences in the predicted present-day and future suitable habitat for the mean-type SDMs were not significant between climate scenarios (Kruskal, p -values $> .14$), except under the present-day conditions

FIGURE 2 Predicted $\log(x + 1)$ -transformed suitable habitat predictions, modelled from 188 coral species using mean-type model predictions across whole WA and nine detailed locations under present-day and four future climate scenarios. CKI—Cocos (Keeling) Islands, CI—Christmas Island, OR—offshore reef NW shelf, KIM—inshore Kimberley, DP—Dampier–Pilbara, NE—Ningaloo–Exmouth Gulf, SB—Shark Bay, HAI—Houtman Abrolhos Islands, WAS—south coast of WA, WA—total coastline of WA. The boxplots represent variability in suitable habitat, while the red circles and notches represent the mean values and 95% confidence interval from the median, respectively



between tropical and tropical/subtropical/temperate range extent ($\chi^2 = 9.75$, p -value $< .01$; see Figure 4). Similarly, classifying the species according to their reproductive mode and life history did not show significant differences in predicted suitable habitat between present-day and the future climate scenarios with the mean-type SDM (Kruskal, p -values $> .05$; see Figure 4). Nevertheless, differences in suitable habitat were significant between genera across the five climate conditions ($F = 2.88$, p -values $< .001$; see Figure S5). For example, the predicted average suitable habitat for corals of the genus *Coscinaraea* increased extensively under $RCP_{8.5}^{2100}$ from present-day conditions ($34,929 \text{ km}^2 \pm 2.66\%$ to $76,079 \text{ km}^2 \pm 2.37\%$), while for *Goniastrea* spp., suitable habitat was also predicted to increase but to a lesser extent ($10,058 \text{ km}^2 \pm 17.04\%$ to $10,579 \text{ km}^2 \pm 30.31\%$; see Figure S5). The suitable habitat and species richness data for genera that are ecologically important with high representative number of species such as *Acropora* and *Montipora* (see Figure S6) indicated that

these genera will struggle at low latitude regions such as the inshore Kimberley and offshore reefs on the NW shelf under $RCP_{8.5}^{2100}$.

3.4 | Regional range extenders and contractors in suitable habitat

Across all the modelled species, 40% and 45% of the species were predicted to experience extreme reductions in suitable habitat ($>90\%$) under $RCP_{8.5}^{2100}$ at the offshore reefs and inshore Kimberley, respectively (see Tables S5 and S6). For example, on the offshore reefs on the NW shelf, species such as *Acropora digitifera*, *Acropora hyacinthus*, *Montipora danae* and *Pocillopora grandis* with a present-day suitable habitat extent of $739 \text{ km}^2 \pm 0.27\%$, $762 \text{ km}^2 \pm 3.47\%$, $570 \text{ km}^2 \pm 17.94\%$ and $451 \text{ km}^2 \pm 43.47\%$, respectively, were predicted to become locally extinct. In the inshore Kimberley, species such as

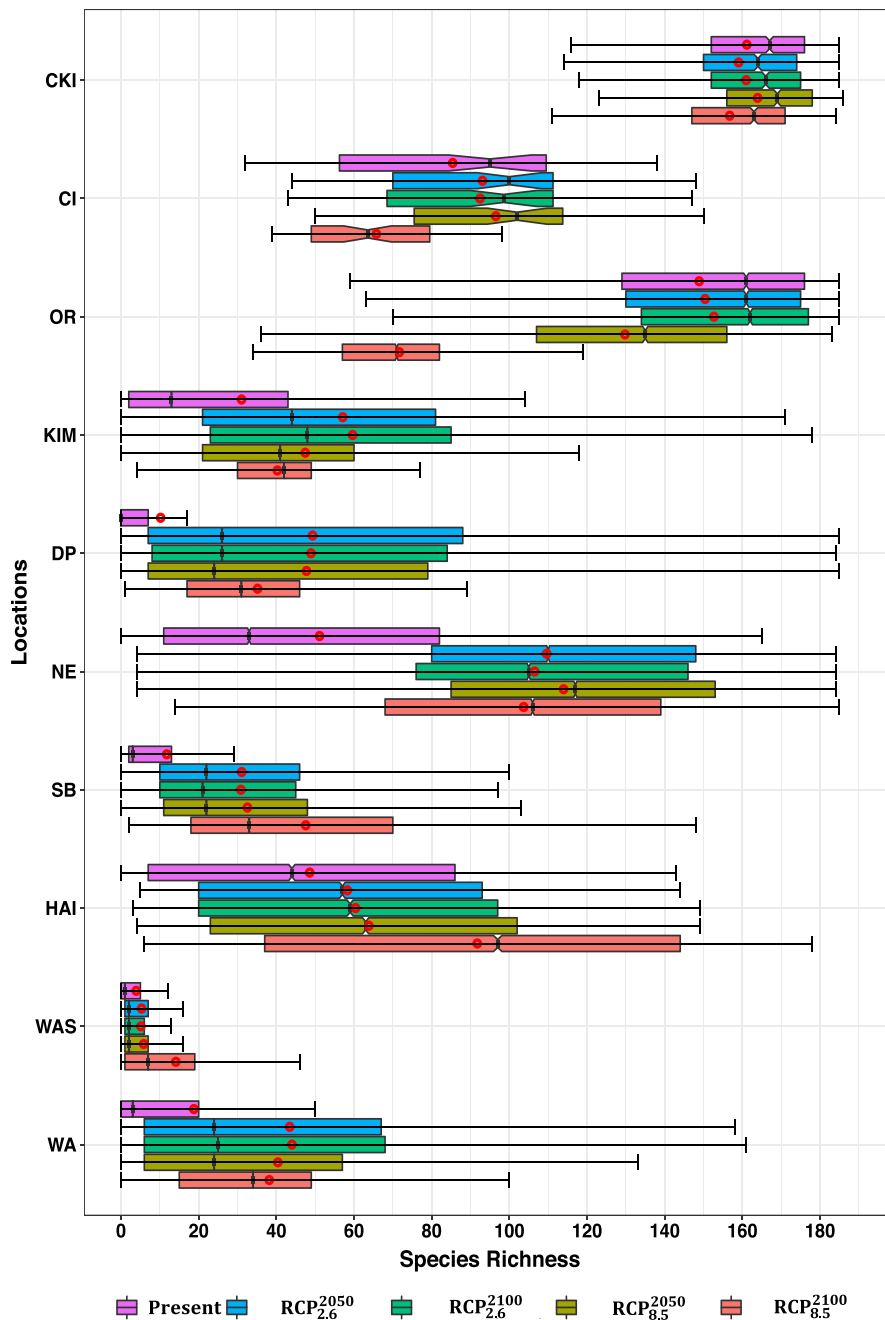


FIGURE 3 Predicted species richness from 188 coral species using mean-type model predictions across WA and nine detailed locations under present-day and four future climate change scenarios. CKI—Cocos (Keeling) Islands, CI—Christmas Island, OR—offshore reef NW shelf, KIM—inshore Kimberley, DP—Dampier–Pilbara, NE—Ningaloo–Exmouth Gulf, SB—Shark Bay, HAI—Houtman Abrolhos Islands, WAS—south coast of WA, WA—Total coastline of WA. Boxplots represent variability in species richness, while red circles and notches represent the mean values and 95% confidence interval from the median, respectively

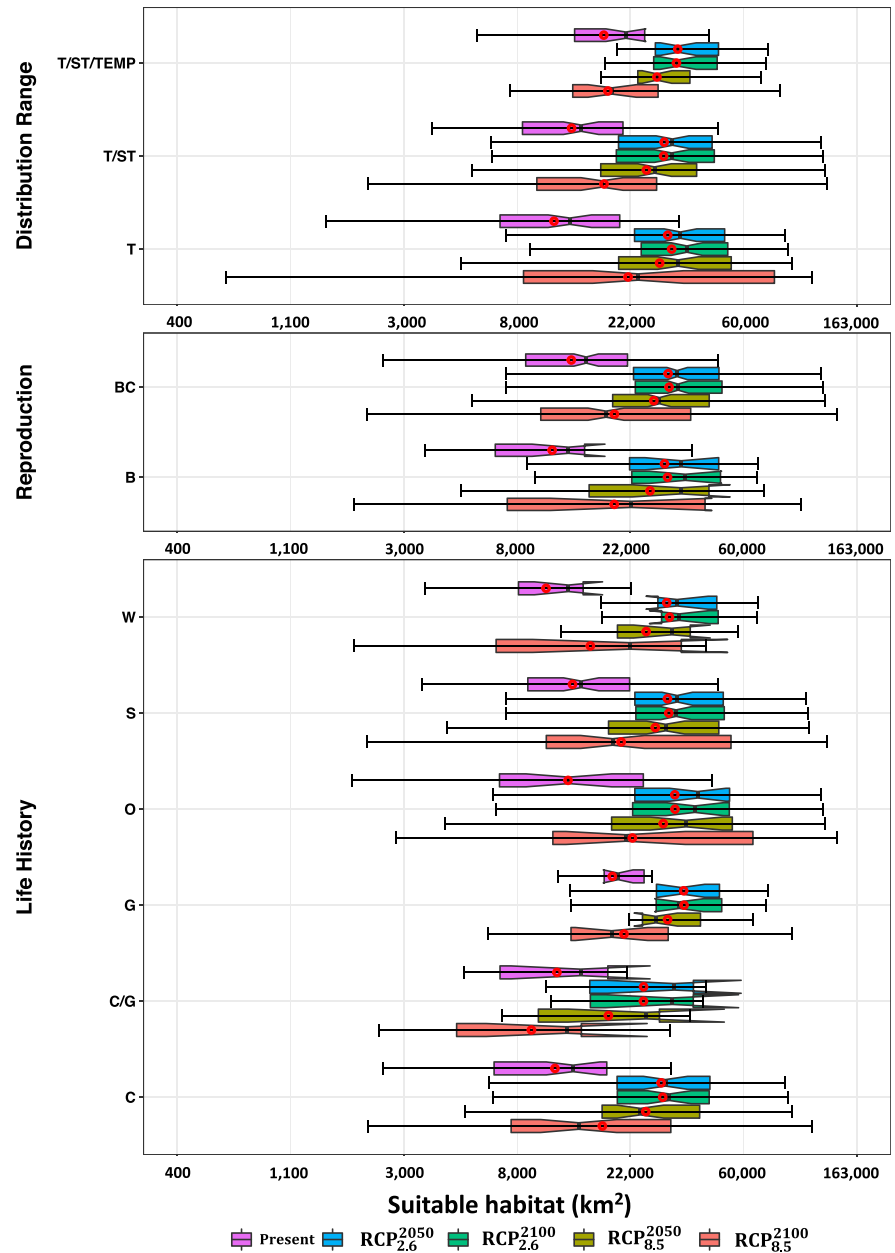
Acropora florida and *Goniopora columna* with a present-day suitable habitat of $4,212 \text{ km}^2 \pm 26.58\%$ and $2,843 \text{ km}^2 \pm 87.43\%$, respectively, were also predicted to disappear (see Table S5). At genera level, genera such as *Astrea*, *Bernardopora* and *Pectinia* were predicted to become regionally locally extinct while 56%, 55%, 40% and 83% of corals of the genus *Acropora*, *Montipora*, *Porites* and *Turbinaria*, represented here by 41, 22, 10 and 6 species, respectively, were predicted to experience at least 90% reduction in suitable habitat in the inshore Kimberley under $\text{RCP}_{8.5}^{2100}$ (see Table S6). Despite regional suitable habitat reductions predicted at low latitude regions, the proportion of competitive, competitive/generalist, stress-tolerant and weedy species, predicted to expand their range >90% at higher latitudes, increased under $\text{RCP}_{8.5}^{2100}$ (see Tables S7 and S8). Specifically, weedy species increased by 78% and 55%, while competitive species increased by 41%

and 20% at Shark Bay and the Houtman Abrolhos Islands, respectively (see Table S7). For example, species such as *Seriatopora hystrix* (weedy) and *Acropora pulchra* (competitive), with a present-day suitable habitat of $91 \text{ km}^2 \pm 0.34\%$ and $2,184 \text{ km}^2 \pm 79.91\%$ were predicted to experience an increase in suitable habitat to $6,875 \text{ km}^2 \pm 33.50\%$ and $12,245 \text{ km}^2 \pm 27.85\%$, respectively, at Shark Bay under $\text{RCP}_{8.5}^{2100}$.

4 | DISCUSSION

We found that suitable habitat was predicted to increase across all regions in WA under both $\text{RCP}_{2.6}^{2050}$ and $\text{RCP}_{2.6}^{2100}$ scenarios with all tropical and subtropical regions remaining coral biodiversity strongholds. Under the extreme $\text{RCP}_{8.5}^{2100}$ scenario, however, a clear tropicalization

FIGURE 4 Predicted $\log(x + 1)$ -transformed suitable habitat modelled from 188 coral species using mean-type model predictions binned into distribution range extent (T—tropical, ST—subtropical, TEMP—temperate), reproductive mode (BC—broadcast spawners, B—brooding) and life history categories (W—weedy, S—stress-tolerant, O—others, G—generalist, C/G—competitive/generalist, C—competitive) under present-day and future climate conditions. Boxplots represent variability in suitable habitat across the categories for specific climate scenario, while red circles and notches represent the mean values and 95% confidence interval from the median, respectively



trend could be observed with coral species expanding their range to mid-high latitude regions, while a substantial drop in coral species richness was predicted at low latitude tropical coral reefs, such as the offshore NW reefs and inshore Kimberley. In the former, present-day coral biodiversity hotspots were predicted to become spatially diluted under RCP²¹⁰⁰_{8.5} scenario. In other words, extensive reductions in present-day coral biodiversity hotspots were predicted in conjunction with limited increased species richness at neighbouring areas in this region (see Figure S4). The spatial dilution and erosion of coral biodiversity at low latitude tropical regions can lead to climate-induced local extinction events that would likely alter the tropical reef composition and impair the functionality of these ecosystem (Vergés et al., 2019).

While suitable habitat and species richness were predicted to expand slightly at mid-high latitude regions under the extreme climate scenario, the extent of increase in species richness at these regions

is not likely to compensate the loss of coral biodiversity at low latitudes. Consequently, the mean level of tropical diversity predicted to be hosted at mid-high latitude regions is substantially lower than present-day tropical diversity hotspots such as those in the inshore Kimberley and offshore reefs. From these results, low latitude tropical reefs are predicted to have diminishing potential to serve as future coral strongholds to preserve tropical coral biodiversity under extreme future climate change conditions.

4.1 | Regional patterns and drivers of biodiversity and suitable habitat change

Our results show that future temperature conditions under RCP²⁰⁵⁰_{2.6} and RCP²¹⁰⁰_{2.6} scenarios would not limit the expansion of coral

biodiversity hotspots in WA. These results are consistent with other studies, which predicted limited reef degradation under slow warming RCP scenarios such as RCP 4.5 (Matz et al., 2020). However, under RCP_{8.5}²⁰⁵⁰ but specifically RCP_{8.5}²¹⁰⁰, two distinct shifts in the range pattern of present-day coral biodiversity hotspots were predicted along the WA coastline. The first is a substantial decline in present-day coral biodiversity hotspots at low latitude tropical regions, particularly in the offshore reefs and inshore Kimberley. In the former, present-day coral biodiversity hotspots were predicted to become spatially diluted under RCP_{8.5}²¹⁰⁰, by virtue of the underlying variability in temperature responses across species (see Figure S7), leading to both predicted gain and extensive reductions in suitable habitat in the inshore Kimberley (see Table S6). A potential explanation for this variability could be that some species are expected to be more resilient to extreme temperature conditions than others with the potential to expand at low latitude tropical regions under RCP_{8.5}²¹⁰⁰. The second pattern that could be observed under RCP_{8.5}²¹⁰⁰ was a clear tropicalization trend whereby tropical species extended their range poleward. Mid- and high latitude locations such as Shark Bay, the Houtman Abrolhos Islands and the south coast of WA were predicted to slightly increase both in biodiversity and in suitable habitat.

The ability for tropical corals to migrate south depends heavily on the ability for those populations to be healthy enough to reproduce, to undertake long-distance dispersal and to settle and survive over multiple generations (Gilmour et al., 2016). All these factors are anticipated to affect species distribution ranges (Matz et al., 2018, 2020). For instance, under all future climate scenarios, Shark Bay was predicted to become a potential future coral biodiversity hotspot. However, most of the area is characterized by unconsolidated sand patches, seagrass meadows and extreme environmental conditions, such as high salinity conditions, which limits the settlement and survival of coral species in the area (Bauman et al., 2015; Lohr et al., 2017). Whether these locations can function as a viable future coral stronghold under continued climate change pressure remains to be seen. The ability of new immigrants to successfully colonize high latitude locations depends on the competitiveness of taxa already present. At the Houtman Abrolhos Islands, for instance, colonization by immigrant taxa will be limited due to a lack of available settlement space owing to fast-growing competitive taxa and the minor contractions in suitable habitat predicted for genera such as *Acropora* (Abdo et al., 2012).

4.2 | Future range extending/contracting coral species

Our predictions indicate that brooding and spawning corals are likely to respond similarly under future scenarios, especially under RCP_{8.5}²¹⁰⁰. Both broadcast spawning corals, which release gametes into the water column, and brooding corals, which produce larvae multiple times a year but have restricted dispersal (Gilmour et al., 2016), were predicted to experience a loss of suitable habitat, particularly

at isolated locations such as the offshore atolls. The observation that reproductive traits are not a major driver of coral distribution changes under climate change complements recent findings that shows the genetic neighbourhood of spawning and brooding corals in the Kimberley to be very similar (Underwood et al., 2020). However, shifts in the preponderance of spawner versus brooder recruits have already been reported (Hughes et al., 2019) and could intensify under climate change conditions.

Based on the predicted changes in habitat suitability, we observed different responses to climate change temperature shifts between species. Comparing range predictions between different life history categories, we found that competitive genera such as *Acropora*, generalists such as *Psammocora* and weedy genera such as *Leptastrea* are candidate range extending species under RCP_{2.6}²⁰⁵⁰ and RCP_{2.6}²¹⁰⁰ conditions (see Table S2). Under RCP_{8.5}²¹⁰⁰, weedy and stress-tolerant species such as *Porites lobata* (Cacciapaglia & van Woesik, 2015) have been expected to become more prevalent under continued increasing temperature conditions (McClanahan et al., 2014). At mid-high latitude regions, all life history groups were predicted to expand their range to some extent. Weedy, stress-tolerant and competitive species can be considered “winners” under global climate change, while fast-growing, competitive genera such as *Acropora* have the potential to disperse over large distances and dominate new areas (Darling et al., 2012). In contrast, species such as encrusting *Coscinaraea columna*, *Porites aranetai*, *Porites vaughani* and *Goniopora pendunculata* could also be considered as successful range expanders (“winners”) under future climate conditions (see Table S8) because of their lower sensitivity to extreme temperature conditions and disturbances in comparison with competitive genera with branching morphology such as *Acropora* (Darling et al., 2012; Loya et al., 2001). At low latitude tropical regions, extensive distribution reductions and regional extinction events of certain taxa were predicted to become more common under RCP_{8.5}²¹⁰⁰. No specific taxa, genera or life history groups were the main drivers in changing distribution patterns under RCP_{8.5}²¹⁰⁰ in the inshore Kimberley region as losses were ubiquitous. Noticeable reductions in suitable habitat were predicted for competitive and competitive/generalist life history genera such as *Acropora* and *Montipora* at low latitude tropical reefs, with *Astrea* and *Bernardopora* predicted to be locally extinct in the inshore Kimberley. Our results also indicate that broadcast coral species such as *Acropora digitifera* and *Acropora tenuis* with distinct population structure at the offshore reefs on the NW shelf (Rosser et al., 2020; Thomas et al., 2020; Underwood, 2009) will almost disappear in the inshore Kimberley and offshore reefs under RCP_{8.5}²¹⁰⁰ conditions (98–100% decrease in predicted suitable habitat; see Table S5). Lower predicted regional species richness combined with highly fragmented available suitable habitat under future climate conditions could affect the resilience of coral communities and increase the likelihood of local extinction events. At present, no coral species are currently listed as threatened under national or state threatened species legislation, and these results show that further consideration of the threatened status of corals at regional scales is warranted.

4.3 | Uncertainty in model predictions and limitations

Our study supports Braunisch et al. (2013) by showing that model performance and suitable habitat predictions are not influenced by the variance in predictor data—implying that most suitable habitat predictions are consistent across the predictor input data. For some regions such as Cocos (Keeling) Islands, inshore Kimberley and Ningaloo–Exmouth Gulf, suitable habitat predictions were significantly different across the three model types under certain future climate conditions (see Figure S8). This may be explained by the high temporal variability of the environmental predictors at those regions. At a species level, the model uncertainty analysis proved invaluable to assess the consistency of predicted local extinction events. For example, coral species *Porites rus* was predicted to undergo substantial reduction in its suitable habitat under $RCP_{8.5}^{2100}$ across the offshore reefs, where the mean model estimated an 84.1% reduction. However, the LB model predicted a 100% reduction (i.e., local extinction), indicating that future environmental conditions could cause potential extinction events that are not captured by models that solely rely on mean predictor data.

Finally, our study showed that variable importance and regional species richness predictions were highly dependent on the selected predictors. For example, the spatial distribution of biodiversity strongholds (future species-rich areas) was different between model types, especially in the Northern Kimberley area under $RCP_{2.6}^{2100}$ and Ningaloo–Exmouth Gulf region under $RCP_{8.5}^{2100}$ (see Figure S8). By integrating a novel model prediction uncertainty analysis based on the temporal variability in environmental variables, we incorporated additional information of the environmental/habitat envelope and limitations in the suitable niche area of the coral species in WA, which increased the accuracy of SDM predictions.

When evaluating the accuracy of model predictions over time and space, it is important to be aware of the assumptions and limitations to interpretation that are associated with SDMs (limitations specific for this study are discussed in the supplementary section). Despite the simplicity of MaxEnt models, these models still provide crucial information of changes in large-scale multispecies distributions under climate change conditions (Barbet-Massin & Jetz, 2014; Huntley et al., 2008; Jones & Cheung, 2015) that are essential to integrate into conservation management (Araújo & Peterson, 2012; Distler et al., 2015; Pearson & Dawson, 2003; Wiens et al., 2009).

4.4 | Broader implications

The degradation and loss of coral reef biodiversity has been predicted and subsequently documented on regional and global scales (Descombes et al., 2015; Freeman et al., 2013; van Hoooidonk et al., 2014; Richards et al., 2021). In this study, we predicted an average of 34% reduction in suitable coral habitat in the inshore Kimberley under $RCP_{8.5}^{2100}$, and similar reductions in suitable reef habitat have been predicted at low latitude regions globally (>32%

reduction for areas where SST > 25 °C; Descombes et al., 2015). Dramatic habitat declines have also been recorded in other marine habitats, such as seagrass meadows (>40% reduction in dense seagrasses in Shark Bay; Strydom et al., 2020) and salt marshes (Saintilan & Williams, 1999; Saintilan et al., 2014). Loss of habitat-forming species in marine hotspots can have significant impacts on other associated species such as fish assemblages (Stuart-Smith et al., 2021). In comparison, range reductions in terrestrial biodiversity hotspots have often been reported to be more extensive due to anthropogenic impacts such as land use and environmental changes, leading to high extinction rates (Brooks et al., 2002; Hu et al., 2021; Kong et al., 2021; Lucas & Harris, 2021).

Our study showed a higher predicted average increase of 51% habitat suitability at mid-latitude regions than a global prediction published for high latitude reefs under $RCP_{8.5}^{2100}$ (0–16%; Descombes et al., 2015). Poleward migration of tropical species has also been predicted and reported for coral species and other marine organisms regionally (Cheung et al., 2012; Hyndes et al., 2016; Stuart-Smith et al., 2021; Tanaka et al., 2012; Tuckett et al., 2017; Vergés et al., 2019; Wernberg et al., 2016; Yamano et al., 2011) and globally (Jones & Cheung, 2015; Lenoir & Svenning, 2015; Pinsky et al., 2020; Poloczanska et al., 2013; Vergés et al., 2014), where areas along poleward western boundary currents are expected to become particularly susceptible to accelerated future warming (Tanaka et al., 2012; Vergés et al., 2014; Wu et al., 2012). Tropicalization not only refers to tropical range expansions but also range contraction of temperate communities (Wernberg et al., 2016), the formation of novel community compositions (Vergés et al., 2014) and in some cases a complete phase shift of community composition (e.g., the replacement of salt-marshes by mangroves; Osland et al., 2013; Saintilan et al., 2014). The poleward range shift of tropical species could threaten endemic temperate ecosystems such as macroalgal communities that currently dominate the south coast of WA. Evidence of high latitude range shifts, contractions of macroalgae, such as kelp-dominated temperate habitats, and ecosystem shifts have been predicted and observed in Australia and around the world. Hence, these results reinforce the findings of others that show tropicalization increases the risk that endemic temperate species may be displaced (Cheung et al., 2012; Tuckett et al., 2017; Vergés et al., 2019; Wernberg et al., 2016). The pattern of tropicalization has more commonly been used to describe latitudinal range shifts in marine systems. This might be related to a higher and diverse dispersal potential of marine organisms (Kinlan & Gaines, 2003), amplifying the movement capacity of the realized niche (Soberón & Nakamura, 2009), which could result in a faster predicted velocity of range shifts as oppose to terrestrial organisms (Burrows et al., 2011).

Our results also showed that competitive, stress-tolerant and weedy species are expected to be particularly successful range extenders due to the impacts of tropicalization. This is consistent with other systems where opportunistic, fast-growing and highly adaptive organisms such as invasive species (Lehmann et al., 2015) or temperature-tolerant species have the potential to expand and colonize new areas (Cook-Patton et al., 2015). In addition, our study

and others showed that species responses to climate conditions can be variable (Chen et al., 2011; Hanberry & Hansen, 2015; Tanaka et al., 2012), where the magnitude of range shifts depends on the combination of multiple factors such as individual physiological responses to selective environmental triggers and biological interactions (Chen et al., 2011). Hence, the rate of tropicalization is expected to be variable across areas and within taxa, resulting in dynamic novel communities at high latitudes (Vergés et al., 2019).

This study predicted greater loss of tropical diversity at low latitudes than gains in species richness at high latitudes regions, which has also been predicted for other coral reef systems (Descombes et al., 2015) and could affect the functionality of future coral refugia at high latitude regions. Climate change refugia are considered to function as buffer zones to counter rapid environmental changes while maintaining diversity and ecosystem services (Morelli et al., 2020). Assessing their capacity and functionality is therefore considered essential when prioritizing refugia for conservation (Keppel et al., 2015). The inshore Kimberley has been suggested to be a tropical refuge for photosymbiotic fauna, but the results of this study cast doubt upon how long this region can function as a biodiversity stronghold. Additionally, estimating the success of climate change refugia is very complex and not only depends on the ability to maintain future biodiversity. Factors such as the potential to sustain ecosystem services while buffering the long-term impacts of climate change such as increasing temperature conditions and ocean acidification (Kavousi & Keppel, 2018) and the potential to cope with indirect impacts such as changes in biotic interactions (Kavousi, 2019) are therefore important to consider. Hence, more research is needed to assess the extent, capacity and persistence of climate change refugia under increasing climate change conditions, particularly at high latitude regions.

5 | CONCLUSIONS

The model predictions described in this study provide a preliminary estimate of the scale of biodiversity changes and extent of suitable habitat shifts that could be expected along the WA coastline under various climate change scenarios. Using SDMs based on museum curated coral records and a selection of environmental and habitat variables, we have predicted a general tropicalization trend and an intensified migration of tropical species to higher latitudes. In 2050 and 2100, temperatures under the most benign climate scenario (RCP 2.6) are not predicted to be the limiting factor for coral growth or survival in WA. Under, RCP_{8.5}²¹⁰⁰ however, offshore atolls and inshore Kimberley are predicted to decrease in overall species richness with 19% and 20% of the species, respectively, disappearing and 26% and 32% gaining suitable habitat at these regions, resulting in a spatial dilution of present-day biodiversity hotspots and a homogenization of diversity levels across the NW shelf. The pronounced loss of both suitable habitat and diversity at low latitude tropical regions is of great concern as these regions are of regional and national significance (Richards et al., 2014, 2015, 2019).

Furthermore, mid-latitude areas such as Ningaloo–Exmouth, Shark Bay and the Houtman Abrolhos Islands were predicted to become future high-diversity refugia where stress-tolerant, weedy but also competitive species are likely to expand their distributional ranges. Drastic biodiversity hotspots losses, the pattern of tropicalization and associated net biodiversity loss at high latitude regions have been reported across different taxa at different spatial scales and have been predicted to intensify under climate change conditions. Therefore, marine organisms are estimated to be more responsive to climate change than terrestrial organisms due to a rapid response to changing climate conditions and the capacity to disperse large distances. As Eastern Indian Ocean reefs reconfigure under climate change, it is likely that novel assemblages will emerge and rare, sensitive or poorly dispersing species may be driven to local extinction. The capacity for these novel climate mid-high latitude assemblages to offset the loss of biodiversity in low latitude regions and their capacity to function as climate change refugia by sustaining important ecological services such as reef building are understudied, and further research using more comprehensive models is warranted.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13400>.

DATA AVAILABILITY STATEMENT

Environmental and geomorphological variables can be found at online databases (sources can be found in Table 1). Coral species

occurrence museum records can be found in the Atlas of Living Australia (<https://www.ala.org.au/>) and upon request at the Western Australian Museum. Coral modelling R script is available for download on the Dryad Digital Repository (<https://doi.org/10.5061/dryad.d51c5b03r>).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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