

RESEARCH ARTICLE

Forecasting climate-driven habitat changes for Australian freshwater fishes

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Abstract

Aims: Climate change is expected to have profound effects on species' distributions into the future. Freshwater fishes, an important component of freshwater ecosystems, are no exception. Here, we project shifts in suitable conditions for Australian freshwater fishes under different climate change scenarios to identify species that may experience significant declines in habitat suitability.

Location: Australia.

Methods: We use MAXENT bioclimatic models to estimate the effect of climate change on the suitable conditions for 154 species of Australian freshwater fishes, of which 109 are endemic and 29 are threatened with extinction. Suitable conditions for freshwater fish species are modelled using three different Earth System climate models (ESMs) under two different emission scenarios to the year 2100. For each species, we examine potential geographic shifts in the distribution of suitable conditions from the present day to 2100 and quantify how habitat suitability may change at currently occupied sites by the end of this century.

Results: Broad-scale poleward shifts in suitable conditions are projected for Australian freshwater fishes by an average of up to 0.38° (~180 km) across all species, depending on the emission scenario. Considerable loss of suitable conditions is forecast to occur within currently recognized distributional extents by 2100, with a mean projected loss of up to 17.5% across species. Predicted geographic range shifts and declines are larger under a high-emission scenario. Threatened species are projected to be more adversely affected than nonthreatened species.

Main Conclusions: Our models identify species and geographic regions that may be vulnerable to climate change, enabling freshwater fish conservation into the future.

KEYWORDS

Australia, conservation, ecological niche modelling, freshwater fishes, MAXENT

1 | INTRODUCTION

Climate regulates the persistence and quality of freshwater environments. Water flow into, and conditions within, freshwater environments are tied to air temperature, precipitation and extreme events such as tropical cyclones and storms (Lough & Hobday, 2011). Freshwater ecosystems are more sensitive to the effects of climate change than terrestrial ecosystems due to their dependence on climate and hydrologic regimes (Morrongiello et al., 2011). Moreover, climate-driven patterns of flow variability can have strong effects on species' occurrence patterns and biodiversity (Kennard et al., 2007; Shelley et al., 2019).

The tight climatic control on freshwater ecosystems suggests precipitation and temperature changes over this century will have large effects (e.g. Hobday & Lough, 2011; Knouft & Ficklin, 2017; Woodward et al., 2016). Shifts in the geographic ranges of freshwater fishes towards higher elevations and latitudes have already been observed in response to recent climate change in both Europe and North America (e.g. Comte & Grenouillet, 2013; Lynch et al., 2016). Freshwater species are particularly vulnerable to changes in climate because their habitat is fragmented and isolated within terrestrial landscapes, with river basins acting as biogeographic islands (Fausch et al., 2002; Olden et al., 2011), limiting dispersal and preventing species from tracking suitable conditions.

Climate change is expected to threaten freshwater environments in Australia, which already experience widespread arid conditions resulting in numerous ephemeral freshwater habitats (Allen et al., 2002; Lough & Hobday, 2011). Rising air temperatures and altered rainfall and streamflow patterns have been observed across the country over the past 50 years, with reduced rainfall in much of southern Australia and increased rainfall in most of the north (CSIRO & The Bureau of Meteorology, 2020). These trends will likely continue; over the next 50 years, climate is projected to become warmer, with country-wide increases in mean annual temperature (Appendix S1). Decreases in cool season rainfall are projected to occur across southern and eastern Australia, increasing drought duration and severity. Conversely, more intense short-duration heavy rainfall events are projected to occur throughout the country (CSIRO & The Bureau of Meteorology, 2020). These changes will likely reduce the area of freshwater habitats and connectivity among them, potentially trapping species in sinking islands of increasingly unsuitable habitat.

Shifts, expansions, and contractions of suitable habitat within freshwater environments can be projected using ecological niche models (ENMs, e.g. Araújo et al., 2019; Bond et al., 2011; Ebner et al., 2016; Ruiz-Navarro et al., 2016). These models, also referred to as species distribution models (SDMs), identify areas of potentially suitable conditions for species based on the correspondence between where a species is found, and the variables hypothesized to constrain a species' distribution. ENMs have applications in species' conservation and management, providing information about expected distributional shifts under climate change, regions of habitat suitability decline, and the potential spread of invasive species (e.g.

Bond et al., 2011; Comte & Grenouillet, 2013; Ebner et al., 2016; Ruiz-Navarro et al., 2016; Warren et al., 2014; West et al., 2016).

Here, we develop a suite of ENMs to project how changing climate will affect suitable abiotic conditions for 154 species of Australian freshwater fishes over the next 80 years. We consider freshwater fish species across the entirety of Australia, a continent characterized by marked regional differences in both climate and freshwater fish diversity (Sternberg & Kennard, 2013; Unmack, 2013). ENMs run on multiple species across a region can provide large-scale forecasts of biodiversity change and allow for freshwater drainage basins to be prioritized for conservation management based on projected habitat decline across taxa. Conservation of freshwater fish biodiversity requires appropriate planning, which in turn requires understanding of the potential effects of climate change on Australia's highly endemic and threatened freshwater fish fauna (Allen et al., 2002; Humphries & Walker, 2013; Le Feuvre et al., 2016; Lintermans et al., 2020). The utility of ecological niche modelling lies in the ability to identify species whose ranges may undergo significant contraction or shifts and whose suitable habitat is projected to move past a dispersal barrier (e.g. beyond a dam, or into an adjacent river basin) and therefore requires managed relocations (Olden et al., 2011).

2 | METHODS

2.1 | Species distribution data

Australian freshwater fish occurrence records were collated from online databases (accessed February 2020), including the Atlas of Living Australia (<https://www.ala.org.au>), Victorian Biodiversity Atlas (<https://vba.dse.vic.gov.au/>), Queensland WildNet database (<https://apps.des.qld.gov.au/species-search/>) and Tasmanian Natural Values Atlas (<https://www.naturalvaluesatlas.tas.gov.au/>). These records were supplemented with data from individual papers (most notably Morgan et al., 1998, 2011; Morgan & Gill, 2004; Pusey et al., 2017; see Table S1 for full list). We filtered occurrence data to remove duplicate or outdated entries (i.e. prior to 1990, the date associated with the expert range maps, see below) and cleaned the data to remove erroneous records (i.e. those outside the accepted range for a species).

Australian freshwater fishes underwent a comprehensive International Union for Conservation of Nature (IUCN) assessment in February 2019, during which up-to-date species distribution maps were produced by a team of experts. These maps (<https://www.iucnredlist.org/>) show the Level 8 hydrobasins (Lehner & Grill, 2013) in which species have been recorded as present since 1990. Level 8 hydrobasins are small watersheds nested within larger river basins and form one of the higher levels of hierarchical basin subdivision following the Pfafstetter coding system (Verdin & Verdin, 1999). The HydroBASINS dataset used here (Lehner & Grill, 2013) was developed in collaboration with IUCN; Level 8 hydrobasins have been used previously to define areas of occupancy for freshwater species in IUCN assessments (<https://www.iucnredlist.org>). The IUCN range

maps were used to clean the occurrence data; that is, occurrences falling outside the ranges on these maps were discarded. This cleaning process was particularly important for removing erroneous Atlas of Living Australia records, known to contain unreliable data. The filtered dataset comprised 78,060 unique records across 245 species (Table S2).

2.2 | Selection of presence and background points

Species' occurrence records (i.e. presence points) were filtered for environmental uniqueness to reduce potential sampling bias (Varela et al., 2014). Any combinations of environmental variables that were nonunique at 1 unit (e.g. mm, °C) resolution were filtered such that only a single occurrence was left. All variables were used to determine environmental uniqueness, and 30,096 records were removed. If an occurrence did not coincide with a grid cell containing climatic values, it was moved a distance of up to 1 km to overlap with the nearest data-complete grid cell using the *nearestLand* function from the 'seegSDM' package v0.1.9 (SEEG Research Group, 2018) in R v4.1.3. This process allowed for the inclusion of occurrences whose coordinates may have been imprecise. Any occurrence more than 1 km from a data-complete grid cell was discarded, which removed 8287 records.

Maxent contrasts presence points against background points when true absence data are unknown (Guillera-Arroita et al., 2014; Merow et al., 2013). We defined the area from which background points were drawn using river basin boundaries (Geoscience Australia, 1997) and IUCN range maps. We sampled background points from drainage divides in which a species is known to be present, determined by IUCN range maps. These sampling areas were chosen to balance the effects of dispersal ability and sampling intensity (Barve et al., 2011; Phillips et al., 2009; VanDerWal et al., 2009). That is, if background points are selected from too large an area (e.g. from different drainage divides than the ones in which a species is known to occur), absences could reflect dispersal barriers rather than habitat suitability. Conversely, if background points are sampled from too small an area (e.g. from only within Level 8 hydrobasins where a species is known to occur), absences may reflect a lack of sampling rather than true absences. Calibration regions for each species are presented in Appendix S2.

2.3 | Selection of climate and topographical variables

We used climate and topographical variables to characterize suitable conditions for freshwater fish species, including 12 topographical and 15 climatic variables. Topographical variables were obtained from the National Environmental Stream Attributes Database v1.1.5 (Stein et al., 2012) at 9 arc-second (approx. 250m) resolution. We included the following variables: aspect (average flow direction), elevation (mean height above sea level), upstream distance (maximum

flow path length upstream to the segment pour point), distance to outlet (flow path length downstream to river mouth or internal drainage), relief (slope of the stream segment), Strahler stream order (an index for classifying streams based on their number of tributaries) and coverage of six vegetation categories (grasses, shrubs, woodlands, forests, bare and other). These variables were chosen because they serve as proxies for flow regime and instream environment, both of which structure habitat suitability for freshwater fishes (Bond et al., 2011; Ebner et al., 2016; Leathwick et al., 2005). For example, distance to outlet can be considered a proxy of salinity, which constrains species' distributions based on salinity tolerance. Although all species considered here are predominantly freshwater, some species are more tolerant of salinity than others and may extend their ranges into brackish waters and tidal reaches of rivers (Allen et al., 2002). Elevation can help to characterize habitat type (e.g. hill streams vs lowland streams) and flow accumulation (low-elevation streams would generally have a greater discharge volume compared with high-elevation streams). Strahler stream order and upstream distance also relate to flow accumulation, and relief and vegetation may provide insight into microhabitats within stream segments. Similar variables have been used previously to model suitable conditions for cling gobies in the Wet Tropics region of Queensland, Australia (Ebner et al., 2016), and for freshwater fishes in Victoria, Australia (Bond et al., 2011).

In addition to topographical variables, we assembled 15 bioclimatic variables at a resolution of 30 arc-seconds (approx. 1 km) from WorldClim (<https://worldclim.org>; Fick & Hijmans, 2017), reflecting aspects of temperature and precipitation. Precipitation patterns are a primary control on the distribution of available freshwater habitat, while surface air temperature correlates with and directly influences water temperature (e.g. Lynch et al., 2016). The effects of temperature on freshwater fish distribution are a reflection of species' individual physiological and life-history traits (see Pusey & Arthington, 2003 for examples and discussion), and these species-specific effects will have implications for biogeography at broader spatial scales. These data were collated in R v4.1.3 (R Core Team, 2022) using the *getData* function in the 'raster' package v3.5.29 (R. J. Hijmans & van Etten, 2012). Topographical layers were mapped onto bioclimatic variables to resample to 30 arc-seconds, ensuring consistent spatial resolution. Resampling relied on bilinear interpolation using the *resample* function in the 'raster' package, except for the Strahler stream index, for which we used nearest neighbour because of its discrete nature.

Collinearity of predictor variables can be particularly problematic when transferring models to new regions and time periods (Dormann et al., 2013). To reduce collinearity in our predictor variables, we implemented two stages of variable selection. First, we tested the strength of correlation between all 12 topographical and 15 bioclimatic variables across Australia. We used Pearson's correlation coefficient (Appendix S3) to remove highly correlated variables (threshold of $|r| = .8$), following Quinn et al. (2014). At this stage, we retained five bioclimatic variables for ecological modelling: annual mean temperature (°C); mean diurnal range of temperature (°C);

temperature seasonality; annual precipitation (mm); and precipitation in the driest quarter (mm). All topographical variables were retained. We then performed variable selection on the 17 remaining variables for each species individually, within the species-specific calibration regions. We calculated variance inflation factors (VIFs) from 5000 randomly selected datapoints across the calibration region of each species using the *vifstep* function from the 'usdm' package v1.1.18 (Naimi et al., 2014). We excluded variables with VIF values >10 (Montgomery & Peck, 1992) through a stepwise procedure, starting with the variable with the highest value. The final sets of variables used in niche modelling for each species are listed in Table S3.

2.4 | Ecological niche modelling

We modelled suitable abiotic conditions for each species (i.e. potential distribution) using Maxent v3.4.3 (Phillips et al., 2006). Maxent is a widely used algorithm that estimates suitable conditions for species from presence-only data by seeking to minimize the entropy between two probability densities: one estimated from the presence data and one from the landscape (Elith et al., 2011). Maxent shows good predictive performance compared with other algorithms (Elith et al., 2006; Merow et al., 2013; Qiao et al., 2015; Townsend Peterson et al., 2007) and is particularly well suited to modelling distributions of rare and elusive species for which only a small number of presence records are available (Pearson et al., 2007; Wisz et al., 2008).

Maxent models were built with the 'dismo' package v1.3.8 (Hijmans et al., 2015) in R v4.1.3. Clamping was turned off following Owens et al. (2013), because it can produce unrealistic response curves at very high or very low values for a variable, which are known to be unsuitable. To optimize models, we used *ENMevaluate* in the 'ENMeval' package v2.0.3 (Kass et al., 2021) to test a range of feature classes and regularization multipliers under fivefold cross-validation for each species. We used three commonly used and recommended feature classes (Linear, Linear Quadratic and Linear Quadratic Hinge) and regularization multiplier values from 1 to 5 (after Feijó et al., 2022). For each species, we selected the combination of feature classes and regularization multipliers that yielded the model with the lowest AIC_c value. The feature classes and regularization multipliers selected for the final Maxent models for each species are listed in Table S3.

We constructed Maxent models for 154 species with occurrences in 13 or more environmentally unique grid cells. This number was chosen so that each training dataset contained 10 or more occurrence points (Pearson et al., 2007; Wisz et al., 2008). The final list of environmentally unique grid cell coordinates that were used in Maxent modelling is presented in Table S4. Model fit was assessed using the continuous Boyce index (CBI; Boyce et al., 2002) and the true skill statistic (TSS; Allouche et al., 2006), given by $TSS = \text{sensitivity} + \text{specificity} - 1$. Sensitivity is defined as the proportion of correctly predicted presences out of all predicted presences, and

specificity as the proportion of correctly predicted absences out of all predicted absences. TSS was calculated based on specificity and sensitivity values at the habitat suitability threshold, which maximizes the sum of these two parameters. We also examined the area under the receiver operating characteristic curve (AUC; Hanley & McNeil, 1982). Evaluation metrics are presented in Table S3. Models were transferred from the calibration region to the entirety of Australia to assess habitat suitability on a continental scale.

We converted suitability to binary presence-absence maps (1 = suitable habitat, 0 = unsuitable) using two threshold methods: 95% least training presence (95% LTP) and maximum sum of sensitivity plus specificity (maxSSS). The former excludes 5% of presence points with the lowest suitability scores and uses the lowest remaining suitability score to threshold the model (Pearson et al., 2007). We used the 95% LTP threshold to account for the possibility that erroneous occurrences were retained within our analyses. MaxSSS uses the threshold value at which the sum of specificity and sensitivity is greatest. Using these binary suitability maps, we estimated the total number of suitable grid cells for each species following Ruiz-Navarro et al. (2016) and calculated the mean latitude and longitude of projected suitable conditions.

2.5 | Future climate scenarios

Present-day models were projected onto six future climate scenarios to generate habitat suitability maps for each species based on the assumption of niche stability over the next 80 years (e.g. Antell et al., 2021; Peterson, 2011; Saupe et al., 2014). We examined the degree to which suitable conditions for freshwater fish species are forecast to change under future climate scenarios using three different Earth System models: CNRM-ESM2-1 (Séférian et al., 2019), ACCESS-ESM1-5 (Ziehn et al., 2020) and MIROC-ES2L (Hajima et al., 2020). We considered both low (SSP 245) and high (SSP 585) emission scenarios for the year 2100. Shared socioeconomic pathways (SSPs) describe trajectories for CO₂ emissions and resulting atmospheric concentrations. Under SSP 245, emissions peak mid-century ~50% higher than year 2000 levels and then decline, whereas emissions continue to increase rapidly and remain high under SSP 585. Current emission trends appear to track projections under a high-emission scenario (Peters et al., 2013; Schwalm et al., 2020).

Future projections of topographical variables were unavailable; instead, present-day topographical variables were used in future projections. Most of these variables refer to physical characteristics of the landscape (e.g. aspect, relief and elevation) that are unlikely to change dramatically in the next 80 years. We recognize other topographical variables, such as Strahler stream index and upstream distance, may change as climate change influences flow regimes. Therefore, our projections from future climate models may be considered as a conservative, 'least change' option in which alterations to river flow are minimal; stream flows and habitat are likely to be disrupted more severely than estimated by our models. Elevation,

while an important predictor variable for some species, was not strongly correlated with climate variables due to our variable selection process and did not cause a systematically different response in models when compared to species for whom elevation is not an important variable.

2.6 | Quantifying effects of climate change on species

We examined change in suitable conditions to 2100 for each species using an ensemble climate model for each emission scenario (SSP 245 and SSP 585) derived from the average prediction across the CNRM-ESM2-1, ACCESS-ESM1-5 and MIROC-ES2L ESMs.

2.6.1 | Projected changes in suitable area

Models were projected across the entirety of Australia to examine habitat suitability change on a continental scale. For each species and emission scenario, the ensemble model was converted to a binary map of suitability using the 95% LTP and maxSSS threshold. Shifts in potentially suitable habitat were calculated by tracking the mean latitude and longitude of suitable grid cells. The total number of suitable grid cells was also calculated to examine changes in the extent of predicted suitable habitat.

2.6.2 | Projected changes in site suitability

For each species, we examined the average change in habitat suitability at sites with known presences and calculated the proportion of sites whose future suitability in 2100 is forecast to drop below the 95% LTP threshold. This metric may help to identify individual species particularly threatened by climate-change-driven habitat loss. We compared the proportion of sites lost between threatened and nonthreatened species using a Mann–Whitney *U* test.

2.7 | Limitations of future niche projections

Our model projections rely on accurate estimates of species' abiotic niches. The correlative modelling performed here may not capture the entirety of a species' fundamental niche (Saupe et al., 2012), particularly if biogeographic barriers have prevented species from occupying all suitable conditions. In such cases, future projections will indicate more change for freshwater fish species than is likely to occur. The robustness of the ENMs also depends on the relative importance of climate and geophysical variables as compared to geographic and biotic ones. Thermal tolerances of many Australian freshwater fishes remain poorly known, and it is possible that geographic and biotic limitations on distributions conceal wider climatic tolerances than reflected in niche estimates. Biotic interactions are

likely to play a role in determining future distributions of species, and competition from invasive species is a known threat to many Australian freshwater fish species (Humphries & Walker, 2013).

Ecological niche model estimates rely on the proper identification of species. Many Australian freshwater fishes are undergoing taxonomic revision, with several candidate species identified. Levels of cryptic speciation within Australian freshwater fishes are high (e.g. Adams et al., 2013; Coleman et al., 2015; Raadik, 2014; Shelley et al., 2018), and taxonomic revisions may reclassify widespread species with broad geographic ranges and climatic niches into multiple species with more restricted geographic ranges and climatic niches. Thus, future taxonomic revisions could increase the proportion of species vulnerable to habitat loss and extinction.

Broadscale projected habitat loss among a small number of widely distributed 'Least Concern' species may arise from the offset between geophysical and climate variables under future scenarios. For example, if suitable climate for species shifts to higher altitudes, these regions may be deemed unsuitable because they fall outside the elevation range occupied by the species in the present day. In these situations, our estimates of future habitat loss may be overly liberal. Further research into physiological requirements and individual dispersal capabilities may aid in discerning the likely implications of climate change on these species.

3 | RESULTS

3.1 | Ecological model performance

Of the 245 species considered, ENMs were constructed for 154 species. The remaining 91 species were characterized by fewer than 13 environmentally unique occurrences (Table S2). Predictive model performance based on TSS was above 0.7 in 121 of 154 species, while CBI was above 0.7 in 109 of 154 species (Table S3). Testing AUC, another commonly used metric of model quality, was above 0.9 (excellent model, after Pearce & Ferrier, 2000) for 131 species and above 0.7 (adequate model) for all species (Table S3).

3.2 | Agreement between climate models

Agreement among ecological models under the different ESMs was quantified for each emission scenario under both the 95% LTP and maxSSS thresholds. Model agreement was estimated by calculating the proportion of grid cells projected to contain suitable conditions under all three climate models out of the total number of grid cells projected to contain suitable conditions for any one climate model. Agreement among climate models was higher for the low-emission scenario (SSP 245) than for the high-emission scenario (SSP 585), regardless of threshold. Reduced agreement among climate models under the high-emission scenario (SSP 585) stems from increased uncertainty associated with this SSP scenario; as climate projections for ESMs diverge, so too will ENM estimates (Porfiriio et al., 2014).

3.3 | Present-day suitable area

The extent of present-day suitable conditions estimated for species ranged from 321 grid cells, or approximately 205 km², under the maxSSS threshold (*Paragalaxias julianus*) to 2,117,620 grid cells, or approximately 1,635,570 km², under the 95% LTP threshold (*Leiopotherapon unicolor*) (Appendix S4). In practice, the area values are likely to be overestimations, as not all grid cells are completely covered by water. Suitable conditions estimated for some species (e.g. *Galaxias auratus* and *Craterocephalus amniculus*) correspond to known geographic ranges (Appendix S5) but extend beyond known distributions for others (Appendix S5). *Galaxias fontanus*, a Critically Endangered species with a restricted distribution within Tasmania, for example, is estimated to have widespread suitable habitat across much of mainland Australia; within Tasmania, however, suitable conditions align reasonably well with the species' observed distribution. Many species endemic to Western Australia (e.g. *Bostockia porosa*, *Galaxias occidentalis* and *Nannoperca vittata*) are projected to have suitable habitat in eastern Australia (Appendix S5); because of this, centroids of potential ranges (Figure 2) often appear closer to the centre of Australia than the centres of their observed distributions.

3.4 | Projected changes in suitable area across Australia

The extent to which climate change was projected to affect suitable conditions varied across the 154 species (Figure 1). Based on ensemble climate models for both high- and low-emission scenarios, potentially suitable area was projected to expand for 32%–37% of

species and to contract for 59%–63% of species by 2100 (Table 1). Between 9 (95% LTP threshold, low-emission scenario) and 14 (maxSSS threshold, high-emission scenario) species were projected to experience a more than 50% increase in suitable area, and between 6 (95% LTP threshold, low-emission scenario) and 17 (maxSSS threshold, high-emission scenario) species were projected to experience a more than 50% decrease in suitable area.

Mean per cent change in suitable area across species was higher in the high- versus low-emission scenario for each threshold. In both emission scenarios, the median per cent change in suitable grid cells was negative, while mean percentage change in suitable grid cells was positive (Table 1). This suggests that a relatively small number of species were projected to undergo disproportionately large range expansions, and the potential for range expansions among these species was greater in the high-emission scenario.

3.5 | Shifts in suitable area under climate change across Australia

Displacement of suitable area was projected to occur primarily poleward under both emission scenarios by 2100 (Figure 2, Table 2, Appendix S6). Northward shifts, however, were projected for 53 species (Table S5) regardless of suitability threshold or emission scenario. These northward range shifts were at least partially driven by loss of currently suitable area in the south, rather than range expansion to the north, consistent with increased temperatures and reduced rainfall projected to occur throughout much of the centre and south of Australia (Preston & Jones, 2006). The average magnitude of shift in suitable conditions was larger under the high- (SSP

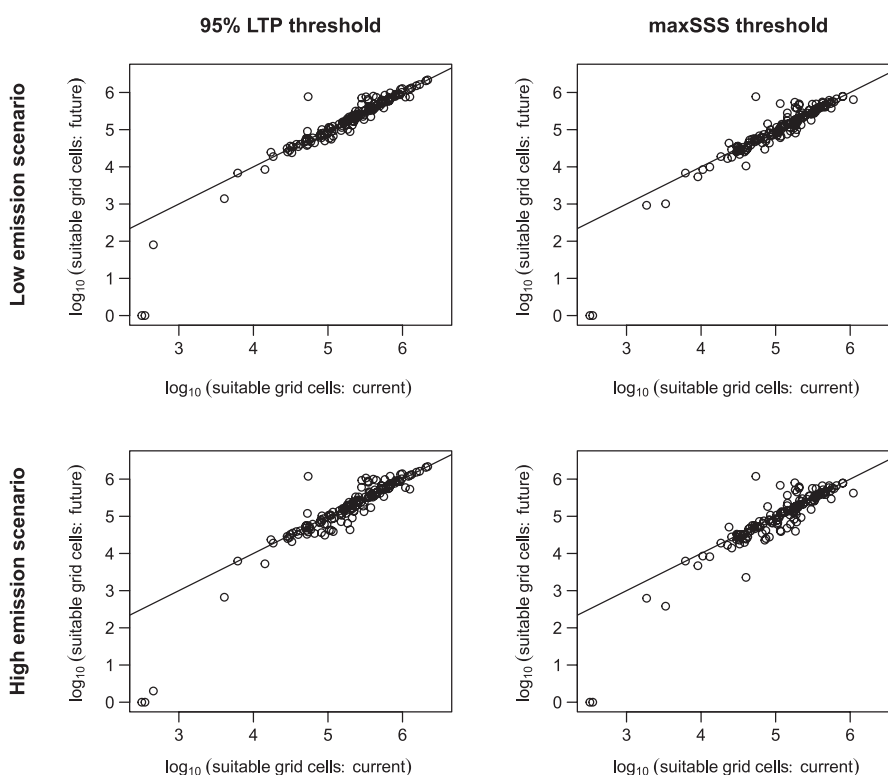


FIGURE 1 Comparison of the number of suitable grid cells under present-day and future conditions using an ensemble ESM for the 154 modelled species.

TABLE 1 Number of species projected to lose or gain suitable grid cells and the mean and median percentage change in grid cell number, under different suitability thresholds using an ensemble climate model for each emission scenario.

Threshold	Emission scenario	No. species with an increase in suitable grid cells	No. species with a decrease in suitable grid cells	Mean % change in suitable grid cells across species	Median % change in suitable grid cells across species
95% LTP	Low	54	100	+6.0	-2.6
	High	57	97	+11.6	-2.2
maxSSS	Low	50	103	+7.3	-3.5
	High	50	103	+13.2	-4.8

Note: Using the maxSSS threshold, one species experienced no change in the number of suitable grid cells.

FIGURE 2 Centroid displacements from present-day to future (2100) suitable conditions for each species under different suitability thresholds using an ensemble climate model for each emission scenario. Arrows in the top left of each figure show the mean direction and 10x the magnitude of change as presented in Table 2. The centroids of potential ranges, shown here, often appear closer to the centre of Australia than do the centroids of species' observed distributions (see Section 3.3).

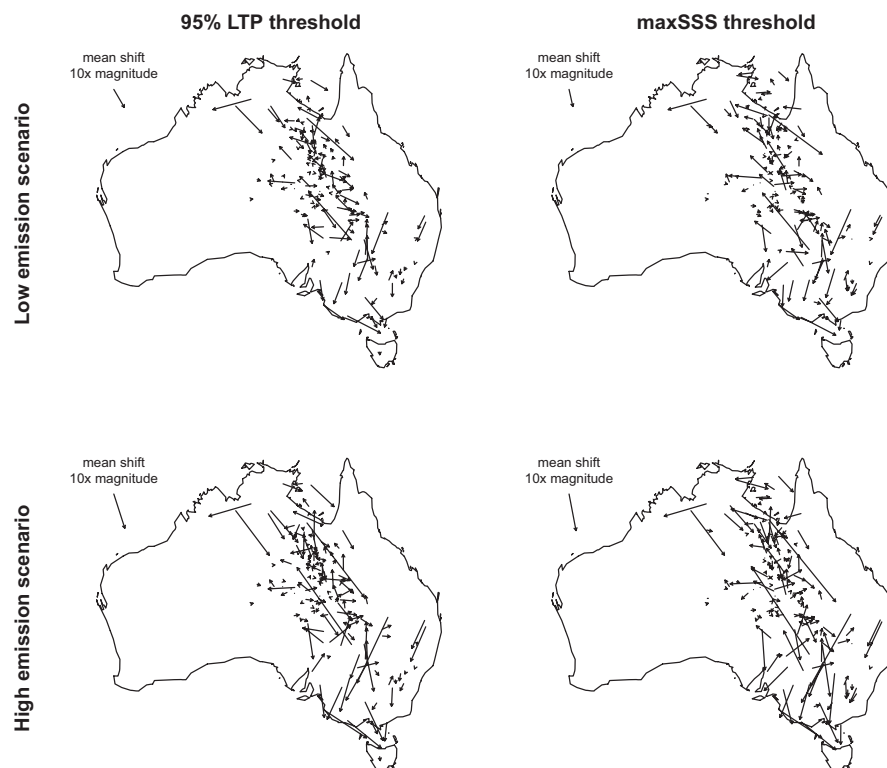


TABLE 2 Mean direction and magnitude of centroid shift in kilometres under different suitability thresholds using an ensemble climate model for each emission scenario.

Threshold	Emission scenario	Mean longitude shift (°)	Mean latitude shift (°)	Mean distance of centroid shift (km)
95% LTP	Low	0.12	-0.19	121
	High	0.13	-0.36	161
maxSSS	Low	0.04	-0.18	136
	High	0.08	-0.38	183

585) rather than the low-emission scenario (SSP 245) and when the maxSSS threshold was used to determine habitat suitability rather than the 95% LTP threshold (Table 2).

3.6 | Projected changes in suitability at presently occupied sites

The extent of suitability decline at present-day occurrence sites varied markedly across species (Figure 3). Using averaged predictions

from the three ESMs for the low-emission scenario, we found that 73% of species were projected to experience a decrease in average habitat suitability (Figure 3a). Across all species, 67.5% are projected to experience an increase in the proportion of sites falling below the present-day 95% LTP (Figure 3b) suitability thresholds. Under the high-emission scenario, 74% of species were projected to experience a decrease in average habitat suitability (Figure 3a). The proportion of species with proportionally more sites falling below the present-day 95% LTP threshold was also higher than in the low-emission scenario (68.2%; Figure 3b). Across all species, the mean

proportion of sites falling below the 95% LTP threshold was 14.0% in the low-emission scenario and 17.5% in the high-emission scenario.

In both emission scenarios, threatened species were projected to experience a greater average decrease in site suitability than non-threatened species (Mann–Whitney U tests, $p < .05$). Threatened species were also projected to have a higher proportion of sites with suitability falling below the 95% LTP threshold when compared to nonthreatened species (Mann–Whitney U tests, $p < .05$).

Some species are projected to lose significant amounts of suitable habitat (Table S6). Depending on the emission scenario, between 11 and 14 species are projected to have more than 50%

of their currently occupied sites fall below the 95% LTP suitability threshold. Of these species, eight are galaxiids and three are percichthyids—both families are major components of Australia's southern temperate freshwater fish fauna. Consistent with these findings, the mean per-species decrease in suitability of occupied sites is greater at higher latitudes, with larger decreases observed across the South West Coast, South East Coast, Murray–Darling and Tasmanian drainage divides (Figure 4). Species that are found in the South East Coast, Tasmania and South West Coast, in particular, also have a higher proportion of sites predicted to drop below the 95% LTP threshold (Figure 4).

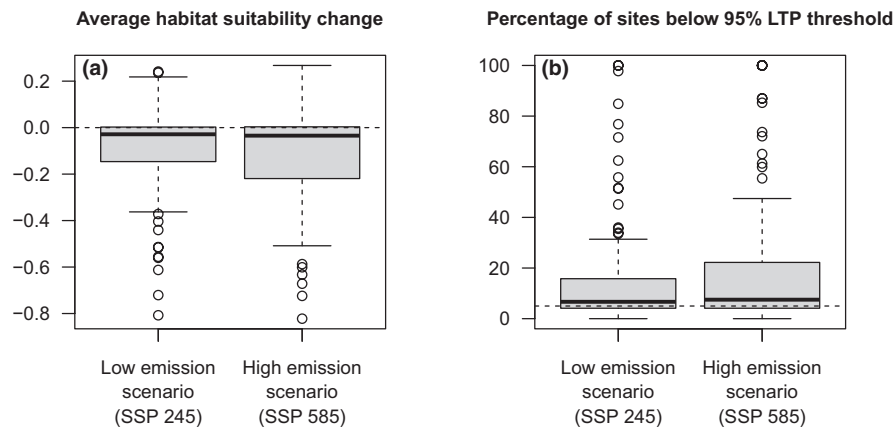


FIGURE 3 (a) Average change in habitat suitability for each species ($n = 154$) at currently occupied sites. Dashed horizontal line represents no change in average habitat suitability. (b) Percentage of sites projected to have a suitability score below the 95% LTP threshold of present-day occurrences for each species, based on an ensemble climate model for each emission scenario. Dashed horizontal line represents the present-day percentage of sites with suitability below the 95% LTP threshold (5% by definition).

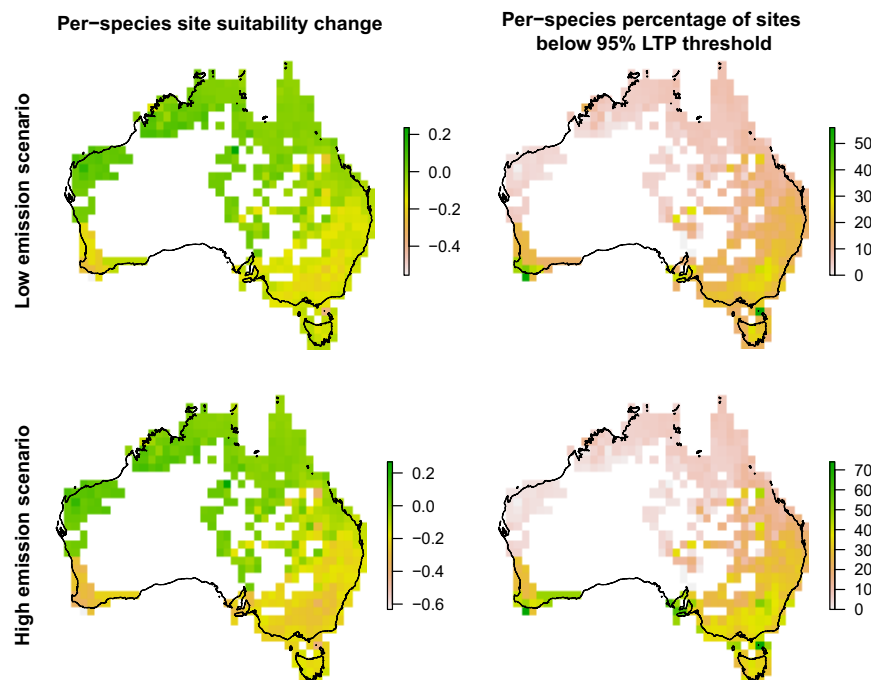


FIGURE 4 Changes to site suitability across Australia in the low-emission (SSP 245) and high-emission (SSP 585) scenarios. Left: the average change in habitat suitability for species occurring in each grid cell. Right: the average percentage of sites projected to have a suitability score below the 95% LTP threshold of present-day occurrences for species in each grid cell.

4 | DISCUSSION

We use ENMs to project potential changes in suitable area for freshwater fish species across Australia under future climate change scenarios. Aquatic and terrestrial species are projected and already observed to favour movement polewards and to higher altitudes as climate changes (e.g. Comte & Grenouillet, 2013; Milanovich et al., 2010; Parmesan & Yohe, 2003; Spence & Tingley, 2020). Our results are congruent with these forecasts and project widespread spatial shifts in a predominantly south to south-east direction (Figure 2).

The effect of climate change on the extent and distribution of suitable conditions varied across species, with some projected to be affected only minimally and others projected to lose large amounts of suitable area. A few species are forecast to experience substantial increases in suitable area, but freshwater fish species are unlikely to expand their distributions given their poor dispersal ability (Radinger et al., 2017). There is as yet limited evidence to suggest Australian freshwater fish species have expanded their ranges as a result of shifting climate, but range contractions have already been documented (Bond et al., 2011). Projections of potential range shifts from ENMs provide a useful baseline from which to conduct more in-depth studies to identify potential refugia to which species could be relocated, designate protected areas, and examine limitations of modelling approaches (Bond et al., 2011).

We examined changes in habitat suitability at locations where species are known to occur today. Over two-thirds of species were projected to experience an average reduction in suitability of occupied habitat. Suitable area was forecast to become increasingly unsuitable in more than 50% of currently occupied sites for 14 species. Of these, six species are listed as Endangered under IUCN red list criteria (*Galaxias auratus*, *Galaxias fontanus*, *Galaxias johnstoni*, *Galaxiella pusilla*, *Nannatherina balstoni* and *Paragalaxias julianus*), two are Vulnerable (*Galaxiella toourtkoourt* and *Maccullochella macquariensis*), and six are Least Concern (*Ambassis agassizii*, *Craterocephalus marjoriae*, *Galaxias brevipinnis*, *Galaxias olidus*, *Melanotaenia fluviatilis* and *Percalates novemaculeata*). The potential loss of suitable area for these threatened species is of particular concern. Climate change and associated habitat loss may further increase extinction risk for species already facing threats from pollution and invasive species. For example, *Galaxias fontanus* has been identified as one of the 22 most endangered species in Australia, with an over 70% chance of going extinct in the next ~20 years (Lintermans et al., 2020). The species has undergone population decline and local extinction due to invasive species and the effects of climate change such as bushfires, droughts, and floods (Lintermans et al., 2020). Of the remaining seven threatened species, all are at risk from invasive species such as brown trout and redfin perch; six are at risk from droughts; five are at risk from dam construction; and two are at risk from bushfires. Dams may threaten species in multiple ways: by acting as barriers and preventing migration of the species; by reducing suitable habitat areas through habitat flooding or water drawdown; or by facilitating the dispersal of invasive predator and competitor species

through altering hydrologic connectivity. These threats are likely to compound the effects of habitat suitability reduction projected by our models.

We found that species occurring at higher latitudes are more likely to be at risk from climate-driven habitat degradation and loss. The average per-species site suitability decrease was larger at higher latitudes (Figure 4); that is, species that are found at higher latitudes were, on average, projected to experience a larger decline in average habitat suitability across their present-day range. Species found at higher latitudes were also projected to have, on average, a higher proportion of currently occupied sites falling below the 95% LTP threshold. Consistent with this geographic pattern, we found that galaxiids and percichthyids were projected to experience the most consistent declines in number of suitable grid cells, the largest average declines in habitat suitability, and the largest number of sites falling below the 95% LTP threshold. Both of these families are major components of Australia's temperate freshwater fish fauna and are widespread across southern mainland Australia and Tasmania.

Reductions in suitability do not necessarily mean that species will not persist at those sites, and our analyses do not include adaptation. Monitoring within areas where the average projected decline is greatest is recommended to determine how species will respond to climate change. Monitoring of individual higher-risk species also may be beneficial to build an understanding of the measurable effects of climate change. Based on the distribution of species projected to suffer the greatest declines in environmental suitability, particularly sensitive areas may include the Australian Alps, East Gippsland, the southwestern coast between Margaret River and Albany, and the lower portion of the Murray River. Although almost all of the species projected to experience the most significant declines are endemic, and many have small ranges, other endemic taxa with similarly-sized ranges were not forecast to experience decreases in environmental suitability. Future studies that explore the relationships between life-history traits and habitat risk may be useful to supplement the approach used here.

We were unable to model 91 species with low numbers of environmentally-distinct occurrences. Many of these species were restricted-range endemics that exist in only a small number of environmentally similar locations. As restricted-range endemics, these species are likely to be particularly vulnerable to shifts in suitable conditions. Thus, our estimates for how freshwater fishes may be affected by shifting climate conditions are likely to be conservative. These species would benefit from high-resolution models that do not employ environmental filtering to identify climatically suitable ranges and how they might change over time (Ebner et al., 2016).

5 | CONCLUSIONS

Quantitative projections of potential occupancy and distributional changes, such as those presented here, provide valuable baseline conservation data that can be tested further and used to inform

conservation strategies. Correlative ecological models do have limitations compared with more in-depth mechanistic approaches (Kearney & Porter, 2009; Peterson et al., 2015), but they provide useful starting points from which to identify higher-priority species or geographic regions for more detailed study. Our modelling shows that, subject to model assumptions, every freshwater fish species could experience reductions in suitable conditions with climate change by 2100. This is of particular concern for already-threatened species.

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CONFLICT OF INTEREST STATEMENT

We have no competing interests.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials. Raw occurrence data were collated from the resources listed in Table S1. Derived data used to construct the ENMs are available in Table S4. Bioclimatic variables for present-day and future climate scenarios are available for download from <https://www.worldclim.org/data/bioclim.html>, and topographical variables are available for download at <https://pid.geoscience.gov.au/dataset/ga/75066>.

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BIOSKETCHES

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Author contributions: Amy R. Tims contributed to conceptualization, formal analysis, investigation, writing—original draft, writing—review and editing, and visualization. Erin E. Saupe contributed to methods, writing—review and editing, and supervision.

SUPPORTING INFORMATION

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

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