







## ORIGINAL ARTICLE

# Genomic Vulnerability to Climate Change of an Australian Migratory Freshwater Fish, the Golden Perch (*Macquaria ambigua*)

Emily J. Booth<sup>1</sup> | Chris J. Brauer<sup>1</sup> | Jonathan Sandoval-Castillo<sup>1</sup> | Katherine Harrison<sup>2,3</sup>  | Meaghan L. Rourke<sup>4</sup> | Catherine R.M. Attard<sup>1</sup>  | Dean M. Gilligan<sup>5</sup> | Zeb Tonkin<sup>3</sup> | Jason D. Thiem<sup>4</sup>  | Peter J. Unmack<sup>6</sup>  | Brenton Zampatti<sup>7</sup>  | Luciano B. Beheregaray<sup>1</sup> 

<sup>1</sup>Molecular Ecology Laboratory, College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia | <sup>2</sup>Department of Environment and Genetics, and Research Centre for Future Landscapes, La Trobe University, Bundoora, Victoria, Australia | <sup>3</sup>Department of Energy, Environment and Climate Action, Arthur Rylah Institute for Environmental Research, Heidelberg, Victoria, Australia | <sup>4</sup>New South Wales Department of Primary Industries Fisheries, Narrandera Fisheries Centre, Narrandera, New South Wales, Australia | <sup>5</sup>Bush Heritage Australia, Melbourne, Victoria, Australia | <sup>6</sup>Centre for Applied Water Science, University of Canberra, Canberra, Australian Capital Territory, Australia | <sup>7</sup>CSIRO Environment, Glen Osmond, South Australia, Australia

**Correspondence:** Luciano B. Beheregaray ([luciano.beheregaray@flinders.edu.au](mailto:luciano.beheregaray@flinders.edu.au))

**Received:** 5 April 2024 | **Revised:** 5 September 2024 | **Accepted:** 25 September 2024

**Handling Editor:** J A H Benzie

**Funding:** This work was supported by Australian Research Council, DP150102903, DP190102533, FT130101068, LP0667952, DE190100636.

**Keywords:** conservation management | ecological genomics | fisheries genomics | genetic rescue | genomic offset | range edge effects

## ABSTRACT

Genomic vulnerability is a measure of how much evolutionary change is required for a population to maintain optimal genotype-environment associations under projected climates. Aquatic species, and in particular migratory ectotherms, are largely under-represented in studies of genomic vulnerability. Such species might be well equipped for tracking suitable habitat and spreading diversity that could promote adaptation to future climates. We characterised range-wide genomic diversity and genomic vulnerability in the migratory and fisheries-important golden perch (*Macquaria ambigua*) from Australia's expansive Murray–Darling Basin (MDB). The MDB has a steep hydroclimatic gradient and is one of the world's most variable regions in terms of climate and streamflow. Golden perch are threatened by fragmentation and obstruction of waterways, alteration of flow regimes, and a progressively hotter and drying climate. We gathered a genomic dataset of 1049 individuals from 186 MDB localities. Despite high range-wide gene flow, golden perch in the warmer, northern catchments had higher predicted vulnerability than those in the cooler, southern catchments. A new cross-validation approach showed that these predictions were insensitive to the exclusion of individual catchments. The results raise concern for populations at warm range edges, which may already be close to their thermal limits. However, a population with functional variants beneficial for climate adaptation found in the most arid and hydrologically variable catchment was predicted to be less vulnerable. Native fish management plans, such as captive breeding and stocking, should consider spatial variation in genomic vulnerability to improve conservation outcomes under climate change, even for dispersive species with high connectivity.

## 1 | Introduction

Anthropogenic climate change is placing unprecedented pressure on biodiversity across the planet (Scheffers et al. 2016; Wiens 2016). Increases in global temperature and changes in precipitation are forcing species to rapidly navigate new conditions that are often beyond their physiological or ecological tolerance (Román-Palacios and Wiens 2020). Species can potentially adjust to climate change via three main non-mutually exclusive mechanisms: dispersal to remain within suitable habitat, phenotypic plasticity, and genetic adaptation (Aitken et al. 2008). However, the ability of a species to realise these responses depends on multiple factors, including habitat connectivity, life history, ecological traits, and levels of standing genomic variation (Garcia et al. 2014; Jarić et al. 2019; Moritz and Agudo 2013).

Highly mobile species have several characteristics that might reduce their vulnerability to climate change compared to those with more limited dispersal abilities. They are often able to track their niche spatially in response to climatic variation and usually show strong gene flow between populations that can result in large effective population sizes and high genetic diversity (Schloss, Nuñez, and Lawler 2012; Shelley et al. 2022). Although high levels of gene flow have traditionally been thought to hinder local adaptation, there is now ample evidence that these evolutionary processes often occur simultaneously (Beheregaray and Sunnucks 2001; Nosil 2012; Tigano and Friesen 2016). Therefore, it is important to recognise that spatially segregated populations of even the most dispersive species can at times be adaptively divergent and show different resilience to climate change (Bay et al. 2018).

Intraspecific variation in climate-related traits, such as thermal or drought tolerance, can arise when populations adapt to their local environment across a climatic gradient (Exposito-Alonso et al. 2019). Populations at the extreme edge of a species' thermal niche are generally subject to stronger selection than those in the core environmental range (Angert, Bontrager, and Ågren 2020). While range-edge populations can incur costs such as reduced population sizes and increased genetic load (Bontrager et al. 2021), divergent adaptive traits may also arise that are well suited to projected climate changes (Lesica and Allendorf 1995; Sandoval-Castillo et al. 2020). Populations currently adapted to warmer conditions might be resilient to climate change if they are able to expand their range into previously cooler areas (Razgour et al. 2019). At the same time, warm range-edge populations might be more likely to experience novel climates or those beyond their thermal limits in the future and could have higher in situ vulnerability to climate change. Understanding which populations will be most threatened under future climates is key for informing management plans (e.g., assisted migration) and prioritising limited conservation resources (Rellstab, Dauphin, and Exposito-Alonso 2021).

Genomic vulnerability (also known as genomic offset) is becoming a popular tool to evaluate the relative sensitivities of intraspecific populations to climate change (Bay et al. 2018; Fitzpatrick and Keller 2015). This evaluation first requires genomic sampling of multiple populations throughout a species' range and using genotype-environment associations (GEAs) to detect statistical relationships between allele frequencies and

current climate conditions. Predictive models are then used to extrapolate or interpolate this relationship to determine the degree of allele frequency change required for a population to maintain current GEAs under projected climates (Capblancq et al. 2020; Rellstab, Dauphin, and Exposito-Alonso 2021). Populations with higher genomic vulnerability are assumed to require larger shifts in allele frequencies (and may even lack certain adaptive variants) to maintain fitness under climate change (Fitzpatrick et al. 2021; Hoffmann, Weeks, and Sgrò 2021). To date, most genomic vulnerability research has focused on terrestrial organisms, and particularly on long-lived tree species (Borrell et al. 2020; Dauphin et al. 2021; Gougherty, Keller, and Fitzpatrick 2021; Gugger et al. 2018). Although a growing number of studies have examined the genomic vulnerability of aquatic taxa (Andrews et al. 2022; Brauer et al. 2023; Nielsen et al. 2021; Tigano et al. 2023), there remains a considerable gap in our knowledge for freshwater species, especially for migratory animals with high gene flow. Freshwater species are particularly vulnerable to climate change since their movement is confined to waterbodies, which are often highly fragmented within the terrestrial landscape and impacted by anthropogenic modifications (Brauer and Beheregaray 2020; Davis et al. 2013). Additionally, for ectothermic aquatic organisms, increases in water temperature are expected to have a large impact on their physiological and developmental functions, and Darwinian fitness (Crozier and Hutchings 2014).

The golden perch (*Macquaria ambigua*) is a medium-large-sized (usually 35–50 cm), long-lived (up to 26 years), and highly dispersive freshwater fish from central and eastern Australia, including one of Australia's most ecologically and socioeconomically important river systems, the Murray–Darling Basin (MDB) (Lintermans 2023). Historical climate change is thought to have played a major role in golden perch evolution, with aridification during the Pleistocene suggested to have driven isolation and lineage divergence across drainage divides (Booth et al. 2022). Golden perch in the MDB are genetically distinct from those in the adjacent Fitzroy, Lake Eyre, and Bulloo-Bancannia drainage basins (Beheregaray et al. 2017; Booth et al. 2022; Faulks, Gilligan, and Beheregaray 2010a, 2010b), although there is evidence of admixture between these lineages (Beheregaray et al. 2017; Booth et al. 2022; Faulks, Gilligan, and Beheregaray 2010a, 2010b). While greater genetic diversity in admixed populations can reduce genomic vulnerability to climate change (Brauer et al. 2023), introgression could introduce maladapted alleles that cause declines in population fitness (Muhlfeld et al. 2009; Todesco et al. 2016), and the management implications of inter-lineage hybridisation for golden perch remain unclear.

In the MDB, golden perch generally prefer warmer lowland habitats but occupy a range of hydroclimatic conditions, from ephemeral arid waterholes to temperate rivers (Attard et al. 2018; Lintermans 2023). The species is capable of large-scale movements across different life history stages (Koehn et al. 2020), with conventional tagging and otolith chemistry showing that adults and juveniles can disperse over extensive distances (100–1000 km) and multiple catchments in association with high river flows (Reynolds 1983; Zampatti et al. 2018). This highly dispersive nature maintains high genetic connectivity, even among contrasting local environments

and geographically distant catchments, as revealed by analyses of mitochondrial DNA, microsatellite, and single nucleotide polymorphism (SNP) markers (Attard et al. 2018; Beheregaray et al. 2017; Booth et al. 2022; Faulks, Gilligan, and Beheregaray 2010a, 2010b). Spawning of golden perch often occurs following long-distance migrations, which are stimulated by increases in temperature and river flows during spring to summer (Ebner, Scholz, and Gawne 2009; King et al. 2016; Koster et al. 2017; Reynolds 1983; Thiem et al. 2022). Genetic diversity in golden perch is positively correlated with spring-time flow, presumably because greater habitat connectivity facilitates movement of both juveniles and adults across the riverscape (e.g., Stuart and Sharpe 2020; Zampatti et al. 2018), leading to higher effective population sizes for reproduction (Faulks, Gilligan, and Beheregaray 2010b). Variation in flow and mean annual temperature have also been linked to adaptive divergence among populations inhabiting climatically defined eco-regions (Attard et al. 2018).

Golden perch have experienced population declines attributed to anthropogenic exploitation, habitat degradation, barriers to movement, flow alteration, and climate change (Cadwallader 1978; Koehn et al. 2020). Since European colonisation, the MDB has been heavily modified for consumptive water use and currently provides potable water for more than 3.6 million people and supports ~40% of Australia's agriculture (Murray-Darling Basin Authority 2021). The construction of barriers such as dams and weirs, alongside unsustainable water extraction, has dramatically changed the natural flow regime and connectivity of the river system (Mallen-Cooper and Zampatti 2018; Walker 2006). These habitat changes are recognised as substantial threats to golden perch recruitment (Lintermans 2023; Stuart and Sharpe 2020). Climate change has further reduced large flow events that facilitate spawning, recruitment, and dispersal (Whetton and Chiew 2021). Increases in the frequency, intensity, and duration of droughts in the MDB (Falster et al. 2024; Whetton and Chiew 2021) have already impacted the species, with millions of fish, including golden perch, dying during hypoxic events over recent years (King, Tonkin, and Lieshcke 2012; Mallen-Cooper and Zampatti 2020; Sheldon et al. 2022). Conservation of golden perch is of broad socioeconomic interest, as it is a culturally important species for Indigenous Australians and a popular target for recreational fishing (and commercial fishing in the Lower Lakes in South Australia) (Balme 1995; Hunt and Jones 2018). Throughout much of the MDB, golden perch populations are supplemented by extensive stocking from hatcheries (Attard et al. 2022b). Ongoing management of the species would benefit from knowledge of its vulnerability to climate change.

Predicting patterns of climate-mediated evolution and vulnerability in migratory animals is a complex task (Bay et al. 2018). In this study, we used a SNP dataset to evaluate range-wide genomic vulnerability to climate change for a migratory freshwater species across a highly environmentally heterogeneous river basin. We first assessed population structure and genetic diversity, then used GEAs to identify loci putatively involved in climate adaptation. We then used gradient forest modelling to predict future mismatches in GEAs and identify the most climate-vulnerable golden perch populations in the MDB. Given the high dispersal capacity of golden perch (Koster et al. 2017;

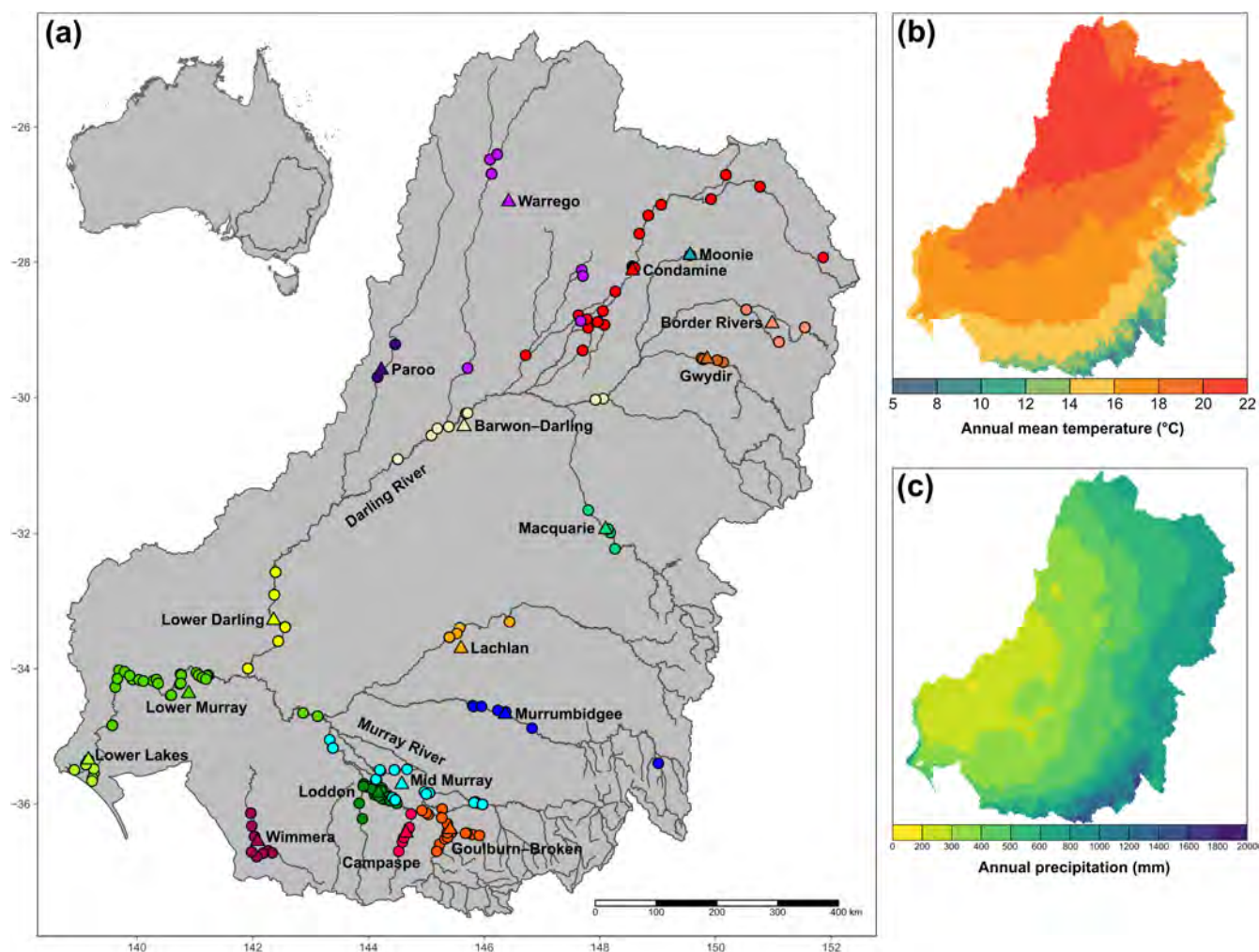
Stuart and Sharpe 2020; Thiem et al. 2022), even geographically distant populations should be expected to exhibit similar levels of standing genomic variation, adaptive variation, and genomic vulnerability to climate change. However, strong selection in response to environmental heterogeneity, particularly at range margins, is expected to generate spatial patterns of adaptive diversity and divergence, even in the presence of gene flow (reviewed in Tigano and Friesen (2016)). Considering the steep hydroclimatic gradient and complex patterns of landscape connectivity found across the MDB (details in Section 2.1 and Figure 1b,c), we predicted spatial variation in genomic vulnerability for golden perch, with populations already living closer to their environmental range limits showing higher vulnerability to projected climates. Our study represents the first assessment of genomic vulnerability to climate change in a migratory freshwater fish. It adds to our understanding of how environmental heterogeneity influences adaptive capacity and highlights the role of gene flow in shaping adaptive divergence. It also provides an exemplar that illustrates the value of integrating evolutionarily-based approaches to improve the management of threatened fisheries resources over modified landscapes.

## 2 | Methods

### 2.1 | Sampling and Genomic Data

The MDB is an expansive river system that covers 1.06 million km<sup>2</sup> of southeastern Australia (Leblanc et al. 2012). It is one of the most variable regions in the world in terms of climate and streamflow, both spatially and temporally (McMahon et al. 2007). Conditions vary from subtropical in the north to semi-arid in the west and temperate in the south (Chiew et al. 2008). Average annual rainfall ranges from > 1500 mm in the southeast to < 300 mm in the west (Chiew et al. 2008). In the north, precipitation is dominated by summer rainfall, whereas in the south, rainfall occurs mostly during winter (Chiew et al. 2008). This regional variation in climate is expected to drive patterns of adaptive genetic diversity in aquatic species distributed across the MDB (Attard et al. 2018; Harrison et al. 2017) and is likely important in determining the vulnerability of populations to climate change.

A total of 1138 golden perch were sampled from ~186 locations in the MDB between 2007 and 2021 (Figure 1). This sampling covered 18 out of 22 catchments of the MDB, capturing the range of climatic conditions experienced by golden perch. We also included 52 golden perch from adjacent drainage basins (Bulloo-Bancannia,  $n = 15$ ; Fitzroy,  $n = 13$ ; Lake Eyre,  $n = 24$ ) to assess the potential for introgression between lineages, as previously reported in other studies (Attard et al. 2022b; Beheregaray et al. 2017). To reduce the risk of sampling stocked individuals, we avoided samples from dams and impoundments, where recruitment is almost completely reliant on stocking (Forbes et al. 2016). Based on results from the ongoing government program FishGen, <4% of the samples used in our study might represent stocked individuals (i.e., had parentage assigned to broodstock fish), which have been found across multiple MDB catchments (Brauer et al., unpublished). Golden perch were caught using a variety of methods, including electrofishing and netting. Caudal fin clips were taken and preserved in 100%



**FIGURE 1** | (a) Map of golden perch sampling sites throughout the Murray–Darling Basin (MDB) in eastern Australia. The 186 sites are coloured based on which catchment they are from (i.e., grouped locations for genomic vulnerability analyses). Circles represent sampling locations, and matching-coloured triangles represent the weighted average sampling location within each catchment (i.e., the locations for which environmental variables were extracted). (b) Annual mean temperature gradient in the MDB and (c) annual precipitation gradient in the MDB (data sourced from [WorldClim.org](https://www.worldclim.org)). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

ethanol at  $-20^{\circ}\text{C}$ , or collected using a commercially available tissue sampling unit (Allflex). DNA was extracted from most samples using a modified salting out protocol (Sunnucks and Hales 1996). Extract quality and quantity were assessed using a NanoDrop 1000 spectrophotometer (Thermo Scientific), gel electrophoresis, and a Qubit fluorometer (Thermo Scientific). For the remaining samples, DNA was extracted by Diversity Arrays Technology (DART) Pty Ltd. DNA was then sent to (or remained at) DART Pty Ltd. for reduced-representation sequencing (DARTseq) and SNP calling (Jaccoud et al. 2001). For SNP calling, the sequenced data was aligned to a publicly available *M. ambigua* reference genome (Dudchenko et al. 2017, 2018; Pavlova et al. 2022).

## 2.2 | Bioinformatics

Bioinformatics and data analyses were performed using R Statistical Software v.4.3.1 (R Core Team 2023). We filtered the raw SNP catalogue using the package “dartR” (Gruber et al. 2018), removing loci with  $>20\%$  missing data and a

minor allele frequency  $<1\%$ . We also excluded individuals with  $>50\%$  missing data. To minimise bias in population structure analyses, we used the package “related” (Pew et al. 2015) to exclude closely related individuals, retaining those with the least missing data (Wang 2002). We removed one sample from each pair with a relatedness value ( $r$ )  $> \sim 0.5$ , to exclude first-order relatives. This was done separately for each major drainage basin (MDB, Bulloo-Bancannia, Fitzroy, and Lake Eyre) to produce four unique datasets. After removing closely related individuals, we combined data from all basins and repeated the missing data filtering to obtain an additional dataset for fastStructure.

## 2.3 | Population Structure

Population structure was assessed using the Bayesian clustering algorithm of fastStructure v.1.0 (Raj, Stephens, and Pritchard 2014). We tested for  $K=1-10$ , with ten replicates per  $K$  value. The best  $K$  value was determined using the Evanno, Regnaut, and Goudet (2005) method, implemented in the

CLUMPAK online server (Kopelman et al. 2015). We used the package “pophelper” (Francis 2017) to visualise the fastStructure results. We ran fastStructure using our whole dataset (including individuals from all four drainage basins), then repeated the analysis with only the MDB individuals for finer scale structure. We also conducted a principal component analysis (PCA) using the package “vegan” (Oksanen et al. 2022) to visualise distinct genetic clusters in the MDB. For PCA, missing genotypes (1.9% of the data matrix) were imputed using the most common genotype for each locus.

## 2.4 | Genetic Diversity

For subsequent analyses, we focused only on the MDB. Since population structure was low in this basin (see Section 3), individuals were grouped by river catchment. Samples from the Lower Lakes, a region of terminal lakes that contrasts to the riverine environment elsewhere, were separated from the broader Lower Murray catchment due to previous evidence of neutral and adaptive divergence in this region (Attard et al. 2018). This regional grouping was done to maximise the range of genotype-environment relationships captured and to ensure predictions of genomic vulnerability can be easily translated into spatially relevant management actions. Based on the filtered SNP dataset for the MDB, measures of genetic diversity (observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ), mean allelic richness (AR), and inbreeding ( $F_{is}$ )) were assessed for each catchment using the package “hierfstat” (Goudet and Jombart 2022). We used a Wilcoxon signed-rank test from the package “stats” (R Core Team 2023) to look for significant differences between catchments. We also calculated pairwise  $F_{ST}$  based on Weir and Cockerham (1984) using dartR, with significance tested using 100 bootstraps, and global  $F_{ST}$  using hierfstat. Genetic diversity ( $H_e$ ,  $H_o$ ,  $F_{ST}$ ) was additionally assessed for a subset of candidate adaptive loci identified by redundancy analysis (see Section 3).

## 2.5 | Genotype-Environment Association Analysis

We downloaded 19 bioclimatic variables from the WorldClim database (Fick and Hijmans 2017) at 2.5 arc-min resolution. These are biologically relevant variables derived from monthly temperature and precipitation values. Although terrestrial-based, such macro-scale variables are considered relevant indicators of local riverine conditions (Frederico, De Marco, and Zuanon 2014) and thus appropriate for studies of teleosts (e.g., Brauer, Hammer, and Beheregaray (2016)). We obtained present-day variables, which reflect average conditions for the years 1970–2000, and variables predicted by the CNRM-CM6-1 model (Voltaire et al. 2019) for three future time points: 2050 (averaged over 2041–2060), 2070 (2061–2080), and 2090 (2081–2100). To define climatic conditions for each catchment, we used an R script to extract variables at a location representing the weighted average of all sampling locations per catchment (Figure 1).

To test for signatures of adaptive diversity in golden perch, we used redundancy analysis (RDA) to identify loci associated with environmental variables. Compared to other GEA analyses, RDA has a lower false-positive and higher true-positive detection rate of adaptive loci (Forester et al. 2018). The predictors in

our RDA were the above-mentioned bioclimatic variables, and catchment level allele frequencies were the response variables. Prior to RDA, variance inflation factor (VIF) analysis was used to reduce the effect of collinearity between bioclimatic variables by removing predictors with a VIF greater than 10. To account for confounding effects of neutral population structure, a matrix of population covariance (omega matrix) was produced using the program BayPass v.2.3 (Gautier 2015). The RDA was then conditioned on synthetic coordinates that were created from the omega matrix using non-metric multidimensional scaling implemented in the package “MASS” (Venables and Ripley 2002). Missing genotypes were imputed using population-specific genotype frequencies based on population structure estimated using the “smnf” function in the package “LEA” (Frichot and François 2015). The significance of the RDA was assessed using the “anova.cca” function of vegan, with 1000 permutations. Candidate adaptive loci were identified as those with scores more than three standard deviations from the mean locus scores for each significant RDA axis.

## 2.6 | Genomic Vulnerability to Climate Change

Genomic vulnerability is an estimate of the amount of genomic change a population will require to maintain current GEAs under projected climate scenarios. We used gradient forest analysis (Fitzpatrick and Keller 2015) to assess genomic vulnerability in golden perch from 18 catchments (including the Lower Lakes region as a separate catchment) of the MDB. Specifically, we used the “gradientForest” package (Ellis, Smith, and Pitcher 2012), following the method of Fitzpatrick and Keller (2015). Gradient forest uses a machine-learning algorithm to predict the turnover of genomic variation as a function of the environment (Ellis, Smith, and Pitcher 2012). Based on their cumulative importance to the model, environmental variables are transformed into “genetic importance” values, and genomic vulnerability is calculated as the Euclidean distance between current and future predicted genetic importance values (Fitzpatrick and Keller 2015).

We ran gradient forest using the candidate loci identified by RDA and the same bioclimatic variables used in the RDA. Genomic vulnerability was estimated for three future time points (2050, 2070, and 2090). For each of these time points, we tested four Shared Socioeconomic Pathways (SSPs), which represent different climate change scenarios that depend on how the world will progress in matters such as population growth, economics, technology, and policy (Schoeman et al. 2023). We included SSP126 (best-case scenario), SSP245 (business-as-usual), SSP370 (intermediate scenario), and SSP585 (worst-case scenario) for a total of 12 different models. We also ran gradient forest on a subset of MDB individuals after removing 178 golden perch that had introgression from adjacent drainage basins (see below).

To evaluate the sensitivity of the gradient forest model to the exclusion of individual catchments, we used a Leave-One-Population-Out (LOPO) cross-validation approach. Models were iteratively fitted by holding out a single catchment from the training data to test the prediction of environmental variables for the excluded catchment. We assessed sensitivity by comparing  $R^2$ , Root Mean Square Error (RMSE), and variable

importance estimates for each LOPO model to the full model and estimated 95% confidence intervals using 1000 iterations. We further examined the distribution of environmental variable predictions for each LOPO model, the full model, and all LOPO models combined.

### 3 | Results

#### 3.1 | Sampling and Genomic Data

DARtseq returned a raw catalogue of 19,871 SNPs for 1190 golden perch (1138 fish from MDB and 52 fish from adjacent drainage basins). For the MDB subset, after filtering, we retained high-quality data for 1049 individuals at 5978 SNPs. This subset was used for the main analyses of the study. Further details of bioinformatic filtering are found in Table S1.

#### 3.2 | Population Structure and Genetic Diversity

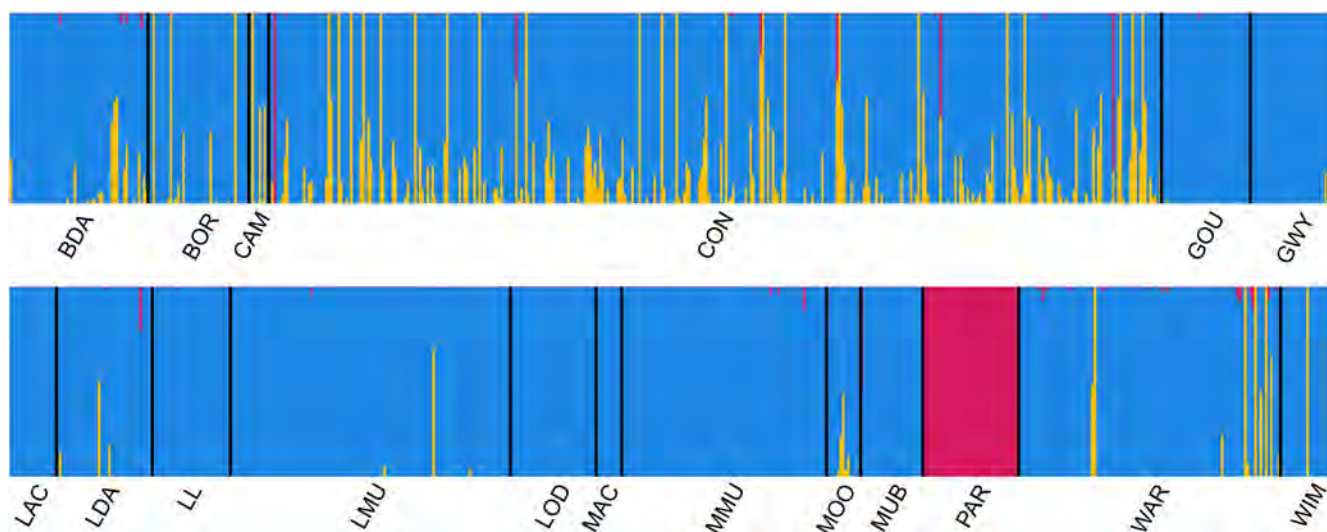
When all four drainage basins were included in the fastStructure analysis, the optimal Delta  $K$  by Evanno, Regnaut, and Goudet (2005) was three, with clusters separating individuals from the MDB, Fitzroy Basin, and Lake Eyre Basin (Figure S3). Golden perch from Bulloo-Bancannia Basin showed intermediate admixture between the MDB and Lake Eyre Basin. We found that 178 individuals from the MDB had introgression from the Lake Eyre and Fitzroy basins (i.e., had <99% MDB ancestry, with maximum hybrid ancestries of 51.4% for Fitzroy and 19% for Lake Eyre). Only one MDB individual was consistent with being an F1 hybrid with the Fitzroy lineage, with others appearing to be later generation backcrosses. For the analysis only using MDB individuals, fastStructure revealed three main clusters. The main metapopulation cluster includes individuals sampled from all catchments except Paroo (PAR), the second cluster distinguishes Paroo, and the third cluster includes individuals mainly from the northern MDB (particularly the Condamine

River)—a pattern likely driven by introgression with the Fitzroy Basin lineage (Figure 2).

Levels of genetic diversity based on all 5978 SNPs were similar (i.e., no significant differences detected by the Wilcoxon signed-rank test) across all catchments in the MDB (Table 1). Expected heterozygosity ( $H_e$ ) ranged from 0.142 to 0.183, observed heterozygosity ( $H_o$ ) ranged from 0.134 to 0.198, allelic richness (AR) ranged from 1.321 to 1.432, and  $F_{IS}$  ranged from  $-0.101$  to  $0.107$  (Table 1). Global  $F_{ST}$  was low (0.011), with the highest pairwise  $F_{ST}$  being 0.05 (Figure S1). The most strongly differentiated were the Paroo (PAR), Lower Lakes (LL), and Moonie (MOO) catchments (Figures S1 and S2). Heterozygosity ( $H_e$  and  $H_o$ ) was higher for the candidate adaptive SNPs compared to the full SNP dataset, but values were still not significantly different between catchments (Table 1).

#### 3.3 | Genotype-Environment Association Analysis

The VIF analysis removed 13 out of 19 bioclimatic variables that inflated model variance. The retained bioclimatic variables used for RDA were mean diurnal range (bio02), isothermality (bio03), minimum temperature of the coldest month (bio06), mean temperature of the driest quarter (bio09), precipitation of the driest month (bio14), and precipitation seasonality (bio15). Overall, the results of the RDA provided evidence for a subtle but significant (full model  $p = 0.035$ ) signal of environmentally constrained genomic variation. The first RDA axis was marginally significant ( $p = 0.089$ ), and permutation tests revealed isothermality as the only significant bioclimatic variable ( $p = 0.032$ ). A total of 119 candidate adaptive SNPs were identified (being more than three standard deviations from the first RDA axis). A strong signal of adaptive divergence was evident for the Paroo (PAR) catchment (Figure 3), which was mainly influenced by isothermality and precipitation seasonality. This suggests that fish in this



**FIGURE 2** | fastStructure results for 1049 golden perch in the Murray–Darling Basin based on 5978 SNPs. Results are shown for  $K = 3$ , the most likely number of clusters determined by the Evanno, Regnaut, and Goudet (2005) Delta  $K$  method. Catchment codes are listed in Table 1. The depicted yellow-colour ancestries indicate admixture between the lineage from the MDB and a lineage from an adjacent drainage basin (see Figure S3 and Attard et al. 2022a for additional details). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 1** | Genetic diversity statistics for golden perch from 18 catchments in the Murray–Darling Basin based on all filtered 5978 SNPs and 119 candidate adaptive SNPs.

Locality code	Catchment	All SNPs					Candidate adaptive SNPs	
		<i>n</i>	$H_e$	$H_o$	$F_{is}$	AR	$H_e$	$H_o$
BDA	Barwon–Darling	56	0.175	0.189	−0.031	1.402	0.386	0.418
BOR	Border Rivers	41	0.171	0.178	−0.012	1.397	0.368	0.380
CAM	Campaspe	8	0.183	0.177	0.023	1.432	0.374	0.361
CON	Condamine	362	0.172	0.156	0.107	1.403	0.361	0.319
GOU	Goulburn–Broken	36	0.154	0.148	0.033	1.352	0.356	0.317
GWY	Gwydir	35	0.169	0.188	−0.066	1.385	0.370	0.408
LAC	Lachlan	18	0.151	0.138	0.073	1.344	0.357	0.318
LDA	Lower Darling	37	0.158	0.151	0.033	1.364	0.355	0.325
LL	Lower Lakes	30	0.153	0.144	0.064	1.347	0.342	0.315
LMU	Lower Murray	108	0.159	0.161	0.011	1.365	0.365	0.361
LOD	Loddon	33	0.153	0.147	0.038	1.350	0.354	0.332
MAC	Macquarie	10	0.156	0.150	0.024	1.358	0.349	0.324
MMU	Mid Murray	79	0.155	0.151	0.025	1.355	0.359	0.337
MOO	Moonie	13	0.172	0.187	−0.046	1.390	0.343	0.402
MUB	Murrumbidgee	24	0.170	0.198	−0.101	1.386	0.381	0.455
PAR	Paroo	37	0.142	0.134	0.049	1.321	0.396	0.375
WAR	Warrego	101	0.162	0.154	0.054	1.374	0.375	0.344
WIM	Wimmera	21	0.157	0.147	0.058	1.362	0.349	0.319

Abbreviations: AR, allelic richness;  $F_{is}$ , inbreeding coefficient;  $H_e$ , expected heterozygosity;  $H_o$ , observed heterozygosity.

catchment may be under strong selection for the extremely variable temperature and precipitation regimes that characterise this arid region. Notable GEAs were also detected for the Lower Lakes (LL) region (temperature-related variables) and the Macquarie (MAC) catchment (mean diurnal range, minimum temperature of the coldest month, and precipitation of the driest month) (Figure 3 and Figure S8).

### 3.4 | Genomic Vulnerability to Climate Change

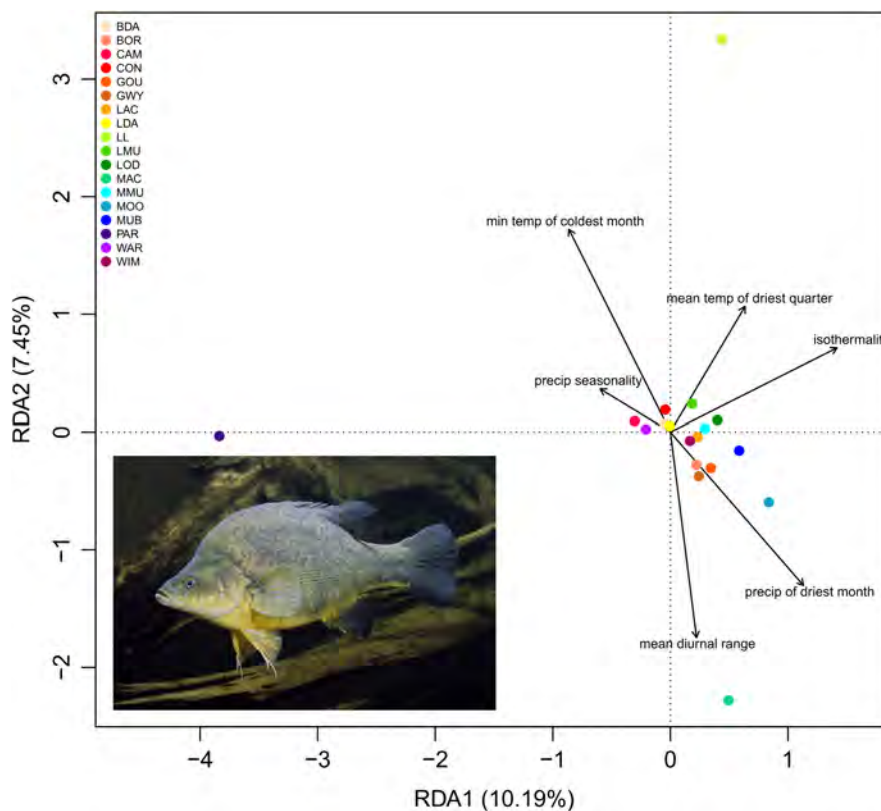
Gradient forest analysis was performed using the 119 candidate loci and the same bioclimatic variables as the RDA. The variable with the greatest accuracy and  $R^2$  weighted importance for adaptive turnover was the minimum temperature of the coldest month (Figure 4). Our genomic vulnerability analysis indicates that golden perch in the most northern MDB catchments (Warrego (WAR), Condamine (CON), Moonie (MOO), Border Rivers (BOR), and Gwydir (GWY)) will experience the greatest genotype–environment mismatch in the coming decades (Figure 5). This pattern holds true across all future time points and SSPs assessed, with the highest genomic vulnerability generally seen in the Warrego catchment (Figure 5). Golden perch in the southern MDB generally have lower genomic vulnerability than those in the north, with the exception

of the Lower Murray (LMU) and Lower Darling (LDA) catchments showing high vulnerability in the milder scenarios (i.e., SSP126–245, and all scenarios in 2050, Figure 5). As expected, the magnitude of genomic vulnerability is shown to increase with time and with more severe climate shifts (Figure S5). Results presented in Figure 5 are based on the analysis that included individuals with partial admixture to the Lake Eyre and Fitzroy basin lineages. Removal of these individuals from the dataset had no clear effect on the genomic vulnerability estimates (Figures S6 and S7).

The Leave-One-Population-Out (LOPO) cross-validation analyses revealed that the environmental variable density distribution curves were similar for all models. All three measures of model performance ( $R^2$ , RMSE, and variable importance) suggested that the basin-wide gradient forest model was relatively insensitive to the exclusion of individual catchments with no evidence for substantial bias associated with any single catchment or environmental variable (Figure 6 and Figures S11, S12).

## 4 | Discussion

Our results indicate that although golden perch maintain high levels of range-wide gene flow, the capacity for populations to



**FIGURE 3** | Redundancy analysis (RDA), testing for genotype-environment associations in golden perch from the Murray-Darling Basin, Australia. Results are based on catchment level allele frequencies at 5978 SNPs. The RDA was constrained on a population covariance matrix created using BayPass. Catchment codes are listed in Table 1. Golden perch photo credit: Gunther Schmida. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

adapt to future climate varies spatially throughout its range. Most golden perch populations living at the warm range edge will require greater evolutionary changes than those in cooler regions to cope with projected climate shifts. However, a relatively isolated and adaptively divergent population in the most arid region, which is already exposed to extreme temperatures and highly variable hydrological regimes, could harbour unique diversity that is pre-adapted to future conditions. These findings have implications for the conservation of migratory aquatic species in fragmented habitats in the face of climate change.

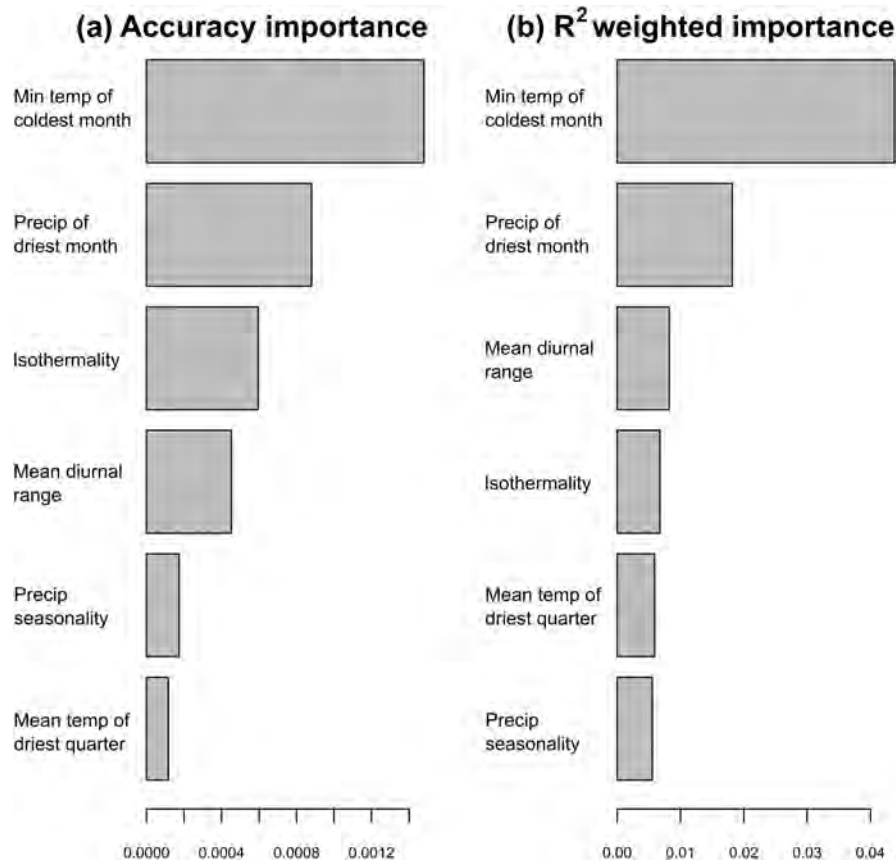
#### 4.1 | A Well-Connected Metapopulation With Divergent Peripheral Populations

Consistent with previous genetic and genomic studies (Attard et al. 2018; Beheregaray et al. 2017; Faulks, Gilligan, and Beheregaray 2010a, 2010b), our results indicate that golden perch in the MDB exist as a well-connected metapopulation with low population structure (e.g., global  $F_{ST}$  is only 0.011). High levels of population connectivity are due to the migratory and dispersive characteristics of the species (Koster et al. 2017; Stuart and Sharpe 2020; Thiem et al. 2022), which has long-distance movements reported across all life history categories (Koehn et al. 2020).

We detected the strongest population differentiation in the Paroo catchment (Figures S1 and S4), in the northwest and most arid region of the MDB. This catchment predominantly exists

as a mosaic of ephemeral waterholes, lakes, and wetlands, only connected to the broader MDB (Darling River) during rare, intense floods. The Moonie catchment in the northeast also showed moderate differentiation (Figure S1). This catchment is also intermittent, and for long periods of the year aquatic organisms are restricted to isolated waterholes (Nixon, Hutchison, and Norris 2022). Golden perch in the Moonie catchment exhibit strong philopatry, moving during periods of high flow then returning to a familiar refugial waterhole to survive drier times (Marshall et al. 2016). In Australian dryland rivers, many aquatic species are adapted to “boom-bust” population cycles to deal with the high variability in climate (Huey et al. 2011). Populations will increase (boom) during times of high flow, when waterbodies are well connected and food resources are abundant, and then decline (bust) as habitat quality reduces during dry phases (Balcombe and Arthington 2009). For example, small subpopulations of desert rainbowfish (*Melanotaenia splendida tatei*) in central Australia are thought to face strong natural selection during periods of isolation but are able to maintain genetic diversity through gene flow during floods (Attard et al. 2022a). We also observed moderate differentiation (Figure S1) of golden perch from the Lower Lakes region (i.e., Lakes Albert and Alexandrina; two large, connected freshwater lakes at the terminus of the MDB). This is likely due to local recruitment in the Lower Lakes occurring alongside gene flow from the Murray River (Attard et al. 2018; Ferguson and Ye 2016). Although golden perch are capable of large-scale movements, they can also exhibit strong site fidelity (Zampatti et al. 2018). Interestingly, all the above examples relate to





**FIGURE 4** | (a) Accuracy importance and (b)  $R^2$  weighted importance of environmental variables in the gradient forest model based on 119 candidate adaptive loci for golden perch from the Murray–Darling Basin, Australia.

peripherally located populations found in regions with divergent hydrological and climatic conditions. This suggests that local environmental conditions, perhaps acting in combination with behavioural, reproductive, and spatial-demographic factors (e.g., Beheregaray and Sunnucks 2001), might be influencing population divergence in peripheral populations of golden perch.

#### 4.2 | Environmental Drivers of Adaptive Diversity

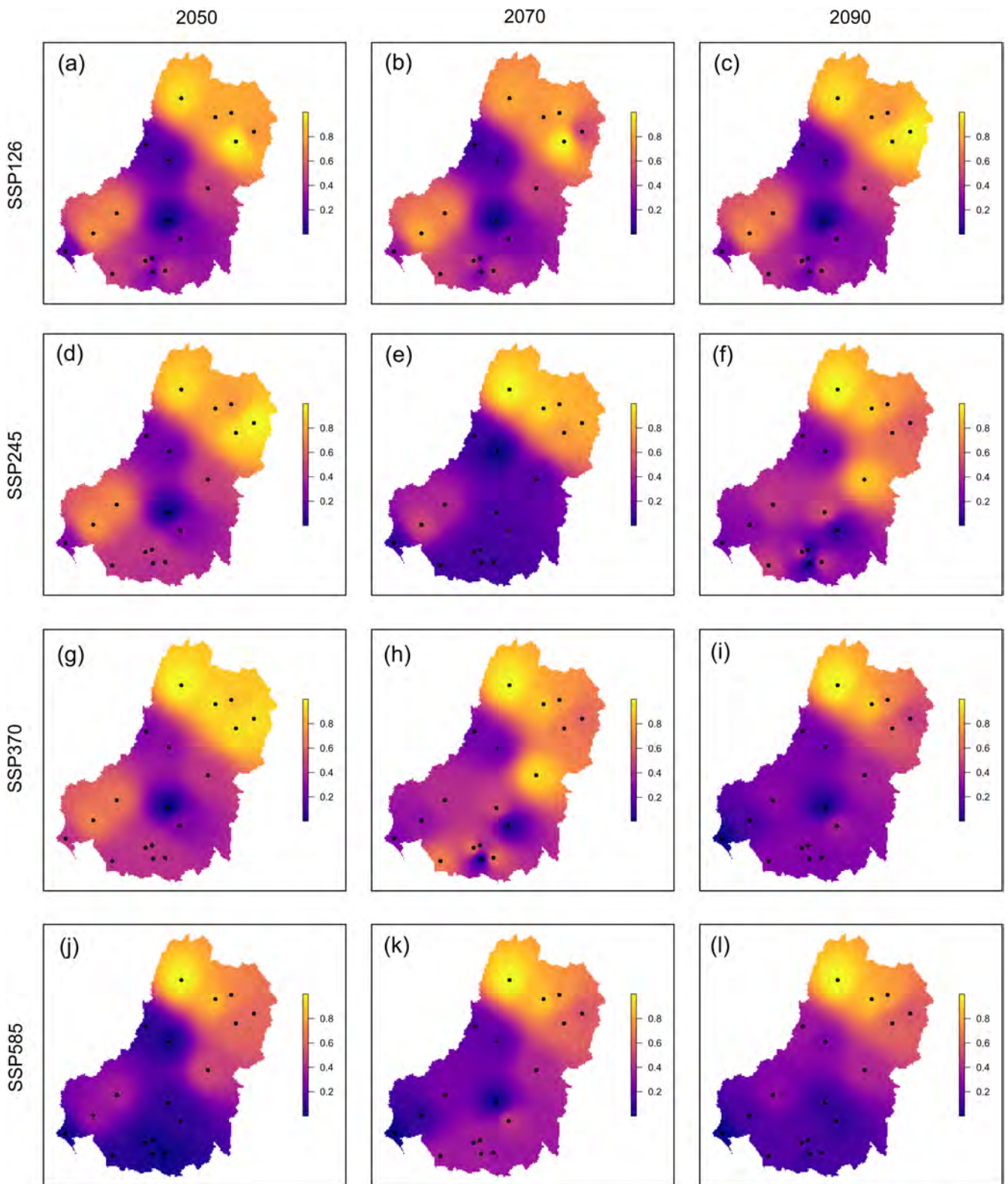
The strongest signals of adaptive divergence were detected in the hydroclimatically distinct Paroo, Lower Lakes, and Macquarie catchments (Figure 3). The strongest predictors of adaptive allele turnover in our gradient forest model were the minimum temperature of the coldest month (bio06) and precipitation of the driest month (bio14) (Figure 4). These environmental proxies for adaptive diversity are consistent with a global meta-analysis of estimated selection gradients (Siepielski et al. 2017) that showed that local and regional variation in climate regime, and in particular precipitation, best explained patterns of selection. Adaptive divergence associated with temperature and precipitation-related variables has been found for other fish species in the MDB (Brauer, Hammer, and Beheregaray 2016; Brauer et al. 2018; Harrison et al. 2017).

Using data from a different reduced-representation sequencing method (ddRAD) and a smaller sample (173 fish), Attard et al. (2018) found that golden perch from the Lower Lakes were

divergent at candidate loci associated with tissue repair, which may be an adaptive response to drought (Attard et al. 2018). The Lower Lakes were severely impacted by the Millennium Drought, which caused water shortages in much of southeastern Australia between 1997 and 2010. Thus, golden perch in the Lower Lakes may harbour critical standing genomic variation that supports persistence through environmentally challenging times (Attard et al. 2018). Variation in streamflow is also known to be a driving force of adaptive divergence in golden perch (Attard et al. 2018). Although we could not directly include streamflow variables in our climate projections, reductions in streamflow due to climate change are expected to have a negative impact on golden perch.

#### 4.3 | Spatial Patterns of Genomic Vulnerability

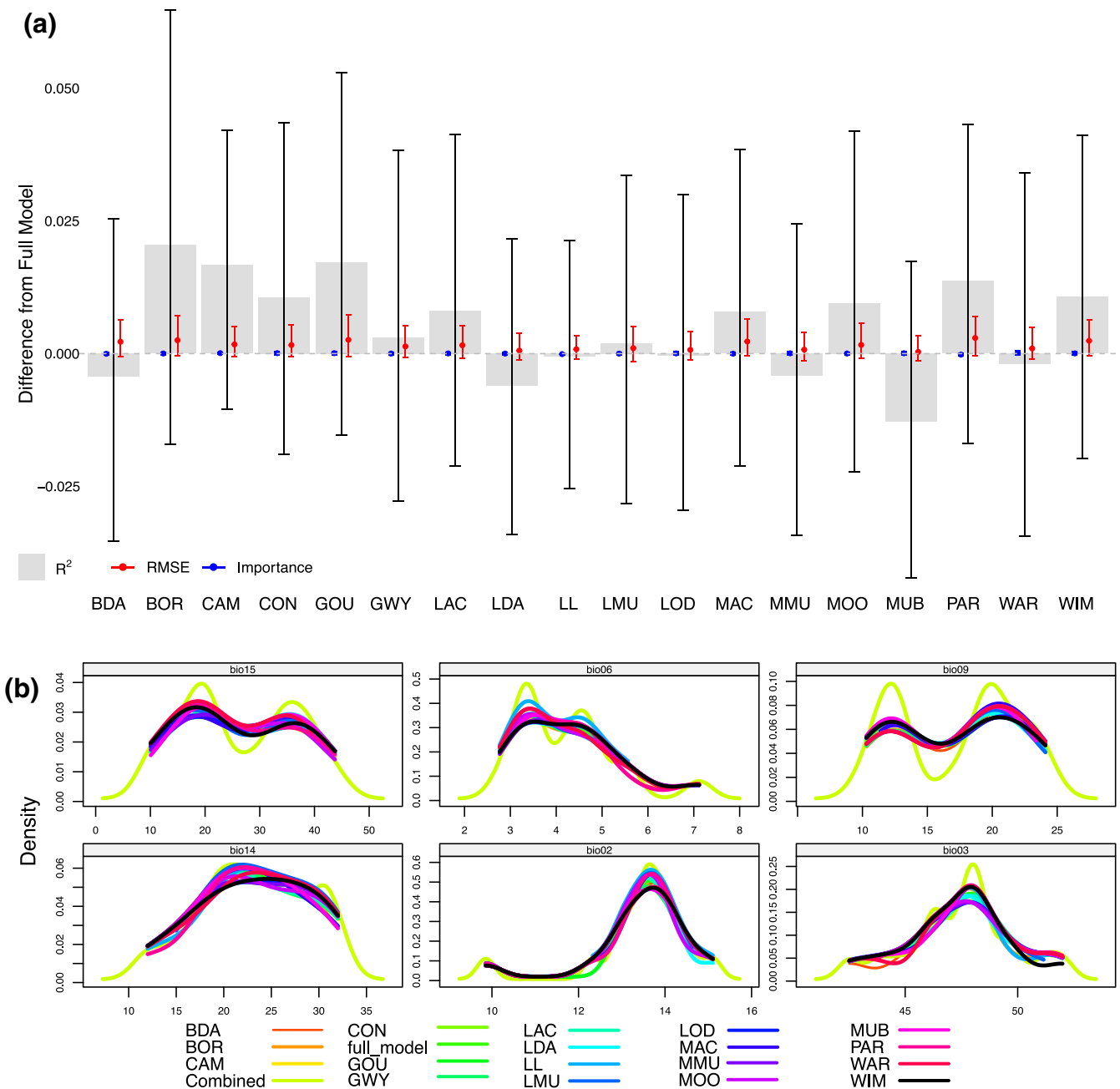
Peripheral populations at geographic or environmental range edges are often simultaneously under strong divergent selection and subject to unique demographic processes related to gene flow and population size (Angert, Bontrager, and Ågren 2020). This can reduce diversity at climate-related genes, which could limit their ability to adapt to climate change (Dauphin et al. 2020; Smith et al. 2020). Populations at warm range edges can be particularly vulnerable to climate change since they might already live closer to their upper thermal limit, but at the same time, these populations potentially hold adaptive diversity that could help other populations adapt to warming conditions (Vranken et al. 2021; Wood et al. 2021). We found



**FIGURE 5** | Genomic vulnerability to climate change for golden perch throughout the Murray–Darling Basin, Australia. Estimated using a gradient forest model based on 119 candidate adaptive loci. Warmer colours (yellow) represent areas of higher genomic vulnerability, where genotype–environment associations are predicted to undergo larger changes in the future. Estimated for three future time points (2050, 2070, and 2090) and four Shared Socioeconomic Pathways (SSP126, SSP245, SSP370, and SSP585). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/mec.17570)]

that golden perch in most of the northern MDB catchments, which are currently exposed to higher annual mean temperatures than those in the south, were predicted to have the highest genomic vulnerability. It is possible that the climate in these

locations will rapidly shift beyond the conditions currently tolerable for golden perch. Species distribution models have similarly predicted that, compared to the rest of the MDB, the northern catchments will face the greatest losses of fish species



**FIGURE 6** | Sensitivity of the full gradient forest model to the exclusion of individual catchments based on a Leave-One-Population-Out (LOPO) cross-validation approach, assessed by (a) difference in  $R^2$  values between the LOPO model and the full model. Positive  $R^2$  suggests improved model fit, while negative  $R^2$  suggests decreased model fit when the population is excluded. RMSE (Root Mean Square Error; red points) shows the mean difference in RMSE between the LOPO model and full model predictions (the environmental variables). Importance (blue points) represents the mean (across all environmental variables) absolute difference in variable importance between each LOPO model and the full model. (b) Density distributions of the environmental variables for each LOPO model, the full model and all LOPO models combined. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

richness under future climates (de Oliveira et al. 2019). The climate shifting beyond optimal conditions in these catchments could have far-reaching impacts for the broader golden perch metapopulation since the northern tributaries are important spawning regions (Stuart and Sharpe 2020).

In contrast to other northern catchments, we found that golden perch in the Paroo catchment have relatively low genomic vulnerability. These results are not due to the possibility that the Paroo might experience fewer climatic changes in the future

compared to other catchments. Substantial changes are predicted for the Paroo (as for the other northern catchments, Figure S9), including future increases in the minimum temperature of the coldest month (Figure S10), which was the most important variable in the gradient forest model. The Paroo catchment experiences the most arid and hydrologically variable climate in the MDB, and golden perch there have likely evolved traits that enable persistence through long periods of drought (Attard et al. 2018; Balcombe et al. 2006). Although the finding of low genomic vulnerability here may seem at odds with the thermal

limits hypothesis, the Paroo is largely isolated from the rest of the MDB. Gene flow can either facilitate or limit adaptation of range-edge populations depending on how the local migration-drift equilibrium mediates natural selection (Angert, Bontrager, and Ågren 2020). On one hand, the combination of low connectivity and extremely challenging environmental conditions in the Paroo suggests that strong selection should promote local adaptation. While relatively small population sizes potentially limit the efficiency of selection, metapopulation dynamics associated with boom-bust climatic cycles in this arid region likely counteract the effects of drift to some degree (*sensu* Attard et al. 2022a). On the other hand, high genomic vulnerability estimates for the northern Warrego, Condamine, Moonie, Border Rivers, and Gwydir catchments may reflect the influence of maladapted gene flow from more temperate regions of the MDB. In this case, despite strong local selection for hotter conditions, high connectivity to the wider MDB could result in genetic swamping of locally adapted alleles (Kirkpatrick and Barton 1997). This suggests golden perch from the Paroo may be an important source of unique adaptive variation for the species in the MDB and should be considered of high conservation value.

We found 178 MDB individuals with partial ancestry to golden perch lineages from either the Fitzroy Basin or the Lake Eyre Basin. These were mainly sampled in the Condamine catchment, which borders the Fitzroy at the northern range edge. Gene flow out of the Fitzroy and Lake Eyre basins could indicate natural connectivity between drainage basins. Contemporary or historical connectivity between Lake Eyre Basin and the MDB has been detected in several other fish species (Attard et al. 2022a; Hughes and Hillyer 2006; Unmack et al. 2023), although observed connectivity between the Fitzroy Basin and the MDB is more rare (Thacker et al. 2007). There is also a strong possibility that these patterns are a sign of human-mediated movement. Although stocking of golden perch across drainage divides is currently prohibited, this likely occurred historically and could still be happening illegally or accidentally (Attard et al. 2022b). Given that golden perch from the MDB, Fitzroy, and Lake Eyre basins are genetically divergent to the point of being considered cryptic species (Beheregaray et al. 2017; Booth et al. 2022; Faulks, Gilligan, and Beheregaray 2010a, 2010b; Musyl and Keenan 1992), there is concern that introgression could be maladaptive. In some cases, introgression between closely related species has been thought to facilitate climate adaptation (Brauer et al. 2023; Turbek et al. 2023). For example, hybrid populations between a warm-adapted and several cold-adapted rainbowfishes (*Melanotaenia*) had lower genomic vulnerability to projected climates compared to pure populations of the cold-adapted species (Brauer et al. 2023). Our genomic vulnerability results here do not reveal any negative impacts of the introgression; however, further investigation is needed to fully understand the potential evolutionary consequences of introgression for golden perch climate change adaptation.

#### 4.4 | Considerations for Genomic Vulnerability Interpretation

Although genomic vulnerability models are becoming increasingly popular and convenient to predict climatic responses and inform decision-making for non-model species, they have

several limitations and often require validation (Bernatchez et al. 2024). An underlying assumption of these models is that present-day populations are optimally adapted to their local environments (Capblancq et al. 2020; Hoffmann, Weeks, and Sgrò 2021; Rellstab, Dauphin, and Exposito-Alonso 2021). In reality, genotype-environment associations are not static through time, and populations can be maladapted to current conditions due to processes such as drift, gene flow, or evolutionary lags in response to recent environmental changes (Brady et al. 2019). These inconsistencies cause potential problems in the interpretation of genomic vulnerability and in understanding how the results relate to population fitness (Lotterhos 2024).

Another caveat of genomic vulnerability pertains to extrapolating optimal allele frequencies to climates not currently observed in the study area (Capblancq et al. 2020; Hoffmann, Weeks, and Sgrò 2021; Rellstab, Dauphin, and Exposito-Alonso 2021). Projecting onto novel climates creates uncertainty in genomic vulnerability estimates, since it is unknown how selective pressures will act on genomic variation in those conditions (Capblancq et al. 2020). Novel climates are expected to become widespread in the future, including in many parts of the MDB. DeSaix et al. (2022) estimated genomic vulnerability of the Brown-capped Rosy-Finch (*Leucosticte australis*) in North America. They highlighted that much of the bird's breeding range will experience novel climates in the coming decades and cautioned the interpretation of genomic vulnerability in these areas.

Predictions of genomic vulnerability can be assessed and validated using carefully designed experiments (e.g., common gardens, reciprocal transplants) (Lotterhos 2024) or long-term monitoring data and integrative functional approaches (Bernatchez et al. 2024). Lower vulnerability was predicted for the Paroo, the most arid catchment and the one shown as indicative of future climate scenarios expected in the remainder of the basin (Balcombe et al. 2011). The Paroo golden perch population is often found in refuge waterholes, requiring adaptations for storing fat to survive during periods of drought and low productivity in this extreme environment (Leigh et al. 2010). Consistent with vulnerability predictions, Attard et al. (2018) found that this is the most adaptively divergent population due to allele frequency differences in genes with functions related to temperature stress and fat storage, including the metabolism of hepatic lipase, bile salt-activated lipase, and neutral cholesterol ester hydrolase 1.

#### 4.5 | Implications for Conservation Management

Genomic vulnerability assessments have the potential to guide conservation practices under climate change (Hoffmann, Weeks, and Sgrò 2021; Rellstab, Dauphin, and Exposito-Alonso 2021). By identifying populations that either possess or lack alleles important for future climate adaptation, this tool could aid in determining source and recipient populations for assisted gene flow (Borrell et al. 2020). Even for species with naturally high gene flow, such as golden perch, human-mediated movement of pre-adapted individuals into more vulnerable populations could be important in facilitating rapid adaptation (Aitken and Whitlock 2013). Golden perch are actively managed for recreational fisheries through extensive stocking programs (Hunt and Jones 2018). The government program FishGen is currently using genomic data from

broodstock to minimise inbreeding and maintain genetic diversity in golden perch hatcheries (Brauer and Beheregaray 2023). The next stages of the FishGen plan are to integrate knowledge of adaptive diversity into stocking practices to improve the resilience of populations under climate change. In this context, we recommend that broodstock could be sourced from the adaptively divergent Paroo catchment, with targeted stocking of this lineage into catchments that show high genomic vulnerability. To weigh the risks of targeted stocking against those of maladaptation under novel climates (Aitken and Whitlock 2013), we recommend studies that experimentally compare thermal tolerance and adaptive plasticity (Sandoval-Castillo et al. 2020) in combination with estimates of vulnerability based on whole genome data (Tigano et al. 2023). The latter can characterise both adaptive SNPs and structural variants, which can play a major role in facilitating local adaptation (Dorant et al. 2020; Wellenreuther et al. 2019) and could be important for rapid evolution under climate change (Layton and Bradbury, 2021).

More broadly, conservation efforts that seek to reinstate or preserve riverscape connectivity throughout the MDB will be important for maintaining high levels of gene flow and genetic diversity within the golden perch metapopulation. There are currently over 10,000 barriers to fish movement (including dams and weirs) throughout the MDB (Baumgartner et al. 2014). The development of fishways that enable fish to traverse these obstacles is important for allowing unrestricted migration of golden perch. Several fishways have already been built along large portions of the Murray River, but fewer have been constructed along the Darling River (Barrett and Mallen-Cooper 2006). Furthermore, mitigating the hydraulic impacts of weir pools will also assist in the downstream dispersal of early life stages (Mallen-Cooper and Zampatti 2020). Efforts of reconnecting golden perch habitat in concert with ecological restoration of waterways would be analogous to implementing human-assisted gene flow for increasing standing genomic variation and adaptive potential (Whiteley et al. 2015). Prioritising a well-connected riverscape through the provision of flows and fishways and establishing climate-ready broodstock populations for stocking programs could aid in reducing the genomic vulnerability of golden perch populations.

Freshwater species are highly threatened by the combination of human impacts and climate change. Understanding how vulnerability to these threatening processes varies across a species range is vitally important for planning effective and efficient conservation actions. For highly mobile species, it is often assumed that little variation exists in adaptive capacity and genomic vulnerability to climate change at the population level. Spatial variation in connectivity, particularly in peripheral, range-edge populations, can however result in divergent evolutionary responses to common selective pressures. This is critically important information for guiding proactive conservation measures such as captive breeding, stocking, and translocations that many species now require.

#### Author Contributions

L.B.B. conceived and supervised the project with assistance from C.J.B. and J.S.C.; L.B.B., J.S.C., K.H., M.L.R., P.J.U., D.M.G., Z.T., J.D.T. and B.Z. obtained samples; E.J.B., C.R.M.A., and K.H. generated the data;

E.J.B. performed data analysis with assistance from C.J.B. and J.S.C.; E.J.B. drafted the manuscript with assistance from L.B.B. and C.J.B.; co-authors revised the manuscript and approved its final version.

#### Acknowledgements

This study used data generated by FishGen, a project funded by the Joint Ventures Monitoring and Evaluation Program (Murray-Darling Basin Authority) and by the Fisheries Research and Development Corporation, as well as data generated with funding from the Australian Research Council, Flinders University, Macquarie University, La Trobe University, The University of Melbourne, and the Goulburn Broken Catchment Management Authority. Financial support was also provided by the Australian Research Council via grants to L.B.B. (LP0667952; FT130101068; DP150102903; DP190102533) and to K.H. (DE190100636). We thank the many people who assisted with curating samples or with fieldwork, including Leanne Faulks, Diana-Elena Vornicu, Kim Shaddick, Julien April, Jon Marshal, Kate Hodges, Doug Harding, Jason Lieschke, Graeme Hackett, Anniq Harris, Wayne Koster, David Dawson, Mark Babbs, Tom Butterfield, Jonathon Doyle, Duncan McLay, Rohan Rehwinkel, Chris Smith, Ian Wooden, Daniel Brooks, Daniel Smith, Chris Bice, David Fleer, George Giatas, Ian Magraith, Adrian Kitchingman, Andrew Pickworth, and Joanne Sharley. Sampling across the MDB was also supported by the CEWO LTIM and EWKR programs and a range of State-based monitoring programs in NSW, Queensland, and Victoria, including the Victorian Environmental Flows Monitoring and Assessment Program.

#### Conflicts of Interest

The authors declare no conflicts of interest.

#### Data Availability Statement

The genomic and environmental data are openly available on figshare: <https://doi.org/10.6084/m9.figshare.27133959.v1>.

#### References

- Aitken, S. N., and M. C. Whitlock. 2013. "Assisted Gene Flow to Facilitate Local Adaptation to Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 44: 367–388. <https://doi.org/10.1146/annurev-ecolsys-110512-135747>.
- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. "Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations." *Evolutionary Applications* 1: 95–111. <https://doi.org/10.1111/j.1752-4571.2007.00013.x>.
- Andrews, K. R., T. Seaborn, J. P. Egan, et al. 2022. "Whole Genome Resequencing Identifies Local Adaptation Associated With Environmental Variation for Redband Trout." *Molecular Ecology* 32: 800–818. <https://doi.org/10.1111/mec.16810>.
- Angert, A. L., M. G. Bontrager, and J. Ågren. 2020. "What Do We Really Know About Adaptation at Range Edges?" *Annual Review of Ecology, Evolution, and Systematics* 51: 341–361. <https://doi.org/10.1146/annurev-ecolsys-012120-091002>.
- Attard, C. R. M., C. J. Brauer, J. Sandoval-Castillo, et al. 2018. "Ecological Disturbance Influences Adaptive Divergence Despite High Gene Flow in Golden Perch (*Macquaria ambigua*): Implications for Management and Resilience to Climate Change." *Molecular Ecology* 27: 196–215. <https://doi.org/10.1111/mec.14438>.
- Attard, C. R. M., J. Sandoval-Castillo, C. J. Brauer, et al. 2022a. "Fish out of Water: Genomic Insights Into Persistence of Rainbowfish Populations in the Desert." *Evolution* 76: 171–183. <https://doi.org/10.1111/evo.14399>.
- Attard, C. R. M., J. Sandoval-Castillo, D. M. Gilligan, P. J. Unmack, L. K. Faulks, and L. B. Beheregaray. 2022b. "Genomics Outperforms Genetics

- to Manage Mistakes in Fisheries Stocking of Threatened Species.” *Biodiversity and Conservation* 31: 895–908. <https://doi.org/10.1007/s10531-022-02369-x>.
- Balcombe, S. R., and A. H. Arthington. 2009. “Temporal Changes in Fish Abundance in Response to Hydrological Variability in a Dryland Floodplain River.” *Marine and Freshwater Research* 60: 146–159. <https://doi.org/10.1071/MF08118>.
- Balcombe, S. R., A. H. Arthington, N. D. Foster, M. C. Thoms, G. G. Wilson, and S. E. Bunn. 2006. “Fish Assemblages of an Australian Dryland River: Abundance, Assemblage Structure and Recruitment Patterns in the Warrego River, Murray–Darling Basin.” *Marine and Freshwater Research* 57: 619–633. <https://doi.org/10.1071/MF06025>.
- Balcombe, S. R., F. Sheldon, S. J. Capon, et al. 2011. “Climate-Change Threats to Native Fish in Degraded Rivers and Floodplains of the Murray–Darling Basin, Australia.” *Marine and Freshwater Research* 62: 1099–1114. <https://doi.org/10.1071/MF11059>.
- Balme, J. 1995. “30,000 Years of Fishery in Western New South Wales.” *Archaeology in Oceania* 30: 1–21. <https://doi.org/10.1002/j.1834-4453.1995.tb00324.x>.
- Barrett, J., and M. Mallen-Cooper. 2006. “The Murray River’s ‘Sea to Hume Dam’ Fish Passage Program: Progress to Date and Lessons Learned.” *Ecological Management & Restoration* 7: 173–183. <https://doi.org/10.1111/j.1442-8903.2006.00307.x>.
- Baumgartner, L., B. Zampatti, M. Jones, I. Stuart, and M. Mallen-Cooper. 2014. “Fish Passage in the Murray–Darling Basin, Australia: Not Just an Upstream Battle.” *Ecological Management and Restoration* 15: 28–39. <https://doi.org/10.1111/emr.12093>.
- Bay, R. A., R. J. Harrigan, V. L. Underwood, H. L. Gibbs, T. B. Smith, and K. Ruegg. 2018. “Genomic Signals of Selection Predict Climate-Driven Population Declines in a Migratory Bird.” *Science* 359: 83–86. <https://doi.org/10.1126/science.aan4380>.
- Beheregaray, L. B., L. V. Pfeiffer, C. R. M. Attard, et al. 2017. “Genome-Wide Data Delimits Multiple Climate-Determined Species Ranges in a Widespread Australian Fish, the Golden Perch (*Macquaria ambigua*).” *Molecular Phylogenetics and Evolution* 111: 65–75. <https://doi.org/10.1016/j.ympev.2017.03.021>.
- Beheregaray, L. B., and P. Sunnucks. 2001. “Fine-Scale Genetic Structure, Estuarine Colonization and Incipient Speciation in the Marine Silverside Fish *Odontesthes argentinensis*.” *Molecular Ecology* 10: 2849–2866. <https://doi.org/10.1046/j.1365-294X.2001.t01-1-01406.x>.
- Bernatchez, L., A.-L. Ferchaud, C. S. Berger, C. J. Venney, and A. Xuereb. 2024. “Genomics for Monitoring and Understanding Species Responses to Global Climate Change.” *Nature Reviews Genetics* 25: 165–183. <https://doi.org/10.1038/s41576-023-00657-y>.
- Bontrager, M., T. Usui, J. A. Lee-Yaw, et al. 2021. “Adaptation Across Geographic Ranges Is Consistent With Strong Selection in Marginal Climates and Legacies of Range Expansion.” *Evolution* 75: 1316–1333. <https://doi.org/10.1111/evo.14231>.
- Booth, E. J., J. Sandoval-Castillo, C. R. M. Attard, D. M. Gilligan, P. J. Unmack, and L. B. Beheregaray. 2022. “Aridification-Driven Evolution of a Migratory Fish Revealed by Niche Modelling and Coalescence Simulations.” *Journal of Biogeography* 49: 1726–1738. <https://doi.org/10.1111/jbi.14337>.
- Borrell, J. S., J. Zohren, R. A. Nichols, and R. J. A. Buggs. 2020. “Genomic Assessment of Local Adaptation in Dwarf Birch to Inform Assisted Gene Flow.” *Evolutionary Applications* 13: 161–175. <https://doi.org/10.1111/eva.12883>.
- Brady, S. P., D. I. Bolnick, A. L. Angert, et al. 2019. “Causes of Maladaptation.” *Evolutionary Applications* 12: 1229–1242. <https://doi.org/10.1111/eva.12844>.
- Brauer, C. J., and L. B. Beheregaray. 2020. “Recent and Rapid Anthropogenic Habitat Fragmentation Increases Extinction Risk for Freshwater Biodiversity.” *Evolutionary Applications* 13: 2857–2869. <https://doi.org/10.1111/eva.13128>.
- Brauer, C. J., and L. B. Beheregaray. 2023. *Final Report for the Murray-Darling Basin Fisheries Genetic Resource Program 2023*. Sydney, NSW: Department of Primary Industries.
- Brauer, C. J., M. P. Hammer, and L. B. Beheregaray. 2016. “Riverscape Genomics of a Threatened Fish Across a Hydroclimatically Heterogeneous River Basin.” *Molecular Ecology* 25: 5093–5113. <https://doi.org/10.1111/mec.13830>.
- Brauer, C. J., J. Sandoval-Castillo, K. Gates, et al. 2023. “Natural Hybridization Reduces Vulnerability to Climate Change.” *Nature Climate Change* 13: 282–289. <https://doi.org/10.1038/s41558-022-01585-1>.
- Brauer, C. J., P. J. Unmack, S. Smith, L. Bernatchez, and L. B. Beheregaray. 2018. “On the Roles of Landscape Heterogeneity and Environmental Variation in Determining Population Genomic Structure in a Dendritic System.” *Molecular Ecology* 27: 3484–3497. <https://doi.org/10.1111/mec.14808>.
- Cadwallader, P. L. 1978. “Some Causes of the Decline in Range and Abundance of Native Fish in the Murray–Darling River System.” *Proceedings of the Royal Society of Victoria* 90: 211–224.
- Capblancq, T., M. C. Fitzpatrick, R. A. Bay, M. Exposito-Alonso, and S. R. Keller. 2020. “Genomic Prediction of (Mal)adaptation Across Current and Future Climatic Landscapes.” *Annual Review of Ecology, Evolution, and Systematics* 51: 245–269. <https://doi.org/10.1146/annurev-ev-ecolsys-020720-042553>.
- Chiew, F. H. S., J. Teng, D. Kirono, et al. 2008. *Climate Data for Hydrologic Scenario Modelling Across the Murray-Darling Basin [A report to the Australian Government from the CSIRO Murray-Darling Basin Sustainable Yields Project]*. Canberra, Australian Capital Territory, Australia: CSIRO.
- Crozier, L. G., and J. A. Hutchings. 2014. “Plastic and Evolutionary Responses to Climate Change in Fish.” *Evolutionary Applications* 7: 68–87. <https://doi.org/10.1111/eva.12135>.
- Dauphin, B., C. Rellstab, M. Schmid, et al. 2021. “Genomic Vulnerability to Rapid Climate Warming in a Tree Species With a Long Generation Time.” *Global Change Biology* 27: 1181–1195. <https://doi.org/10.1111/gcb.15469>.
- Dauphin, B., R. O. Wüest, S. Brodbeck, et al. 2020. “Disentangling the Effects of Geographic Peripherality and Habitat Suitability on Neutral and Adaptive Genetic Variation in Swiss Stone Pine.” *Molecular Ecology* 29: 1972–1989. <https://doi.org/10.1111/mec.15467>.
- Davis, J., A. Pavlova, R. Thompson, and P. Sunnucks. 2013. “Evolutionary Refugia and Ecological Refuges: Key Concepts for Conserving Australian Arid Zone Freshwater Biodiversity Under Climate Change.” *Global Change Biology* 19: 1970–1984. <https://doi.org/10.1111/gcb.12203>.
- de Oliveira, A. G., D. Bailly, F. A. S. Cassemiro, et al. 2019. “Coupling Environment and Physiology to Predict Effects of Climate Change on the Taxonomic and Functional Diversity of Fish Assemblages in the Murray–Darling Basin, Australia.” *PLoS One* 14: e0225128. <https://doi.org/10.1371/journal.pone.0225128>.
- DeSaix, M. G., T. L. George, A. E. Seglund, G. M. Spellman, E. S. Zavaleta, and K. C. Ruegg. 2022. “Forecasting Climate Change Response in an Alpine Specialist Songbird Reveals the Importance of Considering Novel Climate.” *Diversity and Distributions* 28: 2239–2254. <https://doi.org/10.1111/ddi.13628>.
- Dudchenko, O., S. S. Batra, A. D. Omer, et al. 2017. “De Novo Assembly of the *Aedes Aegypti* Genome Using Hi-C Yields Chromosome-Length Scaffolds.” *Science* 356: 92–95. <https://doi.org/10.1126/science.aal3327>.
- Dudchenko, O., M. S. Shamim, S. S. Batra, et al. 2018. “The Juicebox Assembly Tools Module Facilitates De Novo Assembly of Mammalian Genomes With Chromosome-Length Scaffolds for Under \$1000.” *bioRxiv*. <https://doi.org/10.1101/254797>.

- Dorant, Y., H. Cayuela, K. Wellband, et al. 2020. "Copy Number Variants Outperform SNPs to Reveal Genotype–Temperature Association in a Marine Species." *Molecular Ecology* 29: 4765–4782. <https://doi.org/10.1111/mec.15565>.
- Ebner, B. C., O. Scholz, and B. Gawne. 2009. "Golden Perch *Macquaria ambigua* Are Flexible Spawners in the Darling River, Australia." *New Zealand Journal of Marine and Freshwater Research* 43: 571–578. <https://doi.org/10.1080/00288330909510023>.
- Ellis, N., S. J. Smith, and C. R. Pitcher. 2012. "Gradient Forests: Calculating Importance Gradients on Physical Predictors." *Ecology* 93: 156–168. <https://doi.org/10.1890/11-0252.1>.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. "Detecting the Number of Clusters of Individuals Using the Software STRUCTURE: A Simulation Study." *Molecular Ecology* 14: 2611–2620. <https://doi.org/10.1111/j.1365-294X.2005.02553.x>.
- Exposito-Alonso, M., H. A. Burbano, O. Bossdorf, R. Nielsen, D. Weigel, and 500 Genomes Field Experiment Team. 2019. "Natural Selection on the *Arabidopsis thaliana* Genome in Present and Future Climates." *Nature* 573: 126–129. <https://doi.org/10.1038/s41586-019-1520-9>.
- Falster, G. M., N. M. Wright, N. J. Abram, A. M. Ukkola, and B. J. Henley. 2024. "Potential for Historically Unprecedented Australian Droughts From Natural Variability and Climate Change." *Hydrology and Earth System Sciences* 28: 1383–1401. <https://doi.org/10.5194/hess-28-1383-2024>.
- Faulks, L. K., D. M. Gilligan, and L. B. Beheregaray. 2010a. "Clarifying an Ambiguous Evolutionary History: Range-Wide Phylogeography of an Australian Freshwater Fish, the Golden Perch (*Macquaria ambigua*)." *Journal of Biogeography* 37: 1329–1340. <https://doi.org/10.1111/j.1365-2699.2010.02304.x>.
- Faulks, L. K., D. M. Gilligan, and L. B. Beheregaray. 2010b. "Islands of Water in a Sea of Dry Land: Hydrological Regime Predicts Genetic Diversity and Dispersal in a Widespread Fish From Australia's Arid Zone, the Golden Perch (*Macquaria ambigua*)." *Molecular Ecology* 19: 4723–4737. <https://doi.org/10.1111/j.1365-294X.2010.04848.x>.
- Ferguson, G. J., and Q. Ye. 2016. *Influences of Drought and High Flow on the Large-Bodied Fish Assemblage in the Lower Lakes [Report to the Department of Environment, Water and Natural Resources, South Australia]*. Urrbrae, SA: SARDI.
- Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Fitzpatrick, M. C., V. E. Chhatre, R. Y. Soolanayakanahally, and S. R. Keller. 2021. "Experimental Support for Genomic Prediction of Climate Maladaptation Using the Machine Learning Approach Gradient Forests." *Molecular Ecology Resources* 21: 2749–2765. <https://doi.org/10.1111/1755-0998.13374>.
- Fitzpatrick, M. C., and S. R. Keller. 2015. "Ecological Genomics Meets Community-Level Modelling of Biodiversity: Mapping the Genomic Landscape of Current and Future Environmental Adaptation." *Ecology Letters* 18: 1–16. <https://doi.org/10.1111/ele.12376>.
- Forbes, J., R. J. Watts, W. A. Robinson, et al. 2016. "Assessment of Stocking Effectiveness for Murray Cod (*Maccullochella peelii*) and Golden Perch (*Macquaria ambigua*) in Rivers and Impoundments of South-Eastern Australia." *Marine and Freshwater Research* 67: 1410–1419. <https://doi.org/10.1071/MF15230>.
- Forester, B. R., J. R. Lasky, H. H. Wagner, and D. L. Urban. 2018. "Comparing Methods for Detecting Multilocus Adaptation With Multivariate Genotype–Environment Associations." *Molecular Ecology* 27: 2215–2233. <https://doi.org/10.1111/mec.14584>.
- Francis, R. M. 2017. "Pophelper: An R Package and Web App to Analyse and Visualize Population Structure." *Molecular Ecology Resources* 17: 27–32. <https://doi.org/10.1111/1755-0998.12509>.
- Frederico, R. G., P. De Marco, and J. Zuanon. 2014. "Evaluating the Use of Macroscale Variables as Proxies for Local Aquatic Variables and to Model Stream Fish Distributions." *Freshwater Biology* 59: 2303–2314. <https://doi.org/10.1111/fwb.12432>.
- Frichot, E., and O. François. 2015. "LEA: An R Package for Landscape and Ecological Association Studies." *Methods in Ecology and Evolution* 6: 925–929. <https://doi.org/10.1111/2041-210X.12382>.
- Garcia, R. A., M. B. Araújo, N. D. Burgess, et al. 2014. "Matching Species Traits to Projected Threats and Opportunities From Climate Change." *Journal of Biogeography* 41: 724–735. <https://doi.org/10.1111/jbi.12257>.
- Gautier, M. 2015. "Genome-Wide Scan for Adaptive Divergence and Association With Population-Specific Covariates." *Genetics* 201: 1555–1579. <https://doi.org/10.1534/genetics.115.181453>.
- Goudet, J., and T. Jombart. 2022. "Hierfstat: Estimation and Tests of Hierarchical F-Statistics." R Package Version 0.5-11.
- Gougherty, A. V., S. R. Keller, and M. C. Fitzpatrick. 2021. "Maladaptation, Migration and Extirpation Fuel Climate Change Risk in a Forest Tree Species." *Nature Climate Change* 11: 166–171. <https://doi.org/10.1038/s41558-020-00968-6>.
- Gruber, B., P. J. Unmack, O. F. Berry, and A. Georges. 2018. "Dartr: An R Package to Facilitate Analysis of SNP Data Generated From Reduced Representation Genome Sequencing." *Molecular Ecology Resources* 18: 691–699. <https://doi.org/10.1111/1755-0998.12745>.
- Gugger, P. F., C. T. Liang, V. L. Sork, P. Hodgskiss, and J. W. Wright. 2018. "Applying Landscape Genomic Tools to Forest Management and Restoration of Hawaiian Koa (*Acacia Koa*) in a Changing Environment." *Evolutionary Applications* 11: 231–242. <https://doi.org/10.1111/eva.12534>.
- Harrisson, K. A., S. J. Amish, A. Pavlova, et al. 2017. "Signatures of Polygenic Adaptation Associated With Climate Across the Range of a Threatened Fish Species With High Genetic Connectivity." *Molecular Ecology* 26: 6253–6269. <https://doi.org/10.1111/mec.14368>.
- Hoffmann, A. A., A. R. Weeks, and C. M. Sgrò. 2021. "Opportunities and Challenges in Assessing Climate Change Vulnerability Through Genomics." *Cell* 184: 1420–1425. <https://doi.org/10.1016/j.cell.2021.02.006>.
- Huey, J. A., D. J. Schmidt, S. R. Balcombe, J. C. Marshall, and J. M. Hughes. 2011. "High Gene Flow and Metapopulation Dynamics Detected for Three Species in a Dryland River System." *Freshwater Biology* 56: 2378–2390. <https://doi.org/10.1111/j.1365-2427.2011.02666.x>.
- Hughes, J. M., and M. J. Hillyer. 2006. "Mitochondrial DNA and Allozymes Reveal High Dispersal Abilities and Historical Movement Across Drainage Boundaries in Two Species of Freshwater Fishes From Inland Rivers in Queensland, Australia." *Journal of Fish Biology* 68: 270–291. <https://doi.org/10.1111/j.0022-1112.2006.01073.x>.
- Hunt, T. L., and P. Jones. 2018. "Informing the Great Fish Stocking Debate: An Australian Case Study." *Reviews in Fisheries Science & Aquaculture* 26: 275–308. <https://doi.org/10.1080/23308249.2017.1407916>.
- Jaccoud, D., K. Peng, D. Feinstein, and A. Kilian. 2001. "Diversity Arrays: A Solid State Technology for Sequence Information Independent Genotyping." *Nucleic Acids Research* 29: e25. <https://doi.org/10.1093/nar/29.4.e25>.
- Jarić, I., R. J. Lennox, G. Kalinkat, G. Cvijanović, and J. Radinger. 2019. "Susceptibility of European Freshwater Fish to Climate Change: Species Profiling Based on Life-History and Environmental Characteristics." *Global Change Biology* 25: 448–458. <https://doi.org/10.1111/gcb.14518>.
- King, A. J., D. C. Gwinn, Z. Tonkin, J. Mahoney, S. Raymond, and L. Beesley. 2016. "Using Abiotic Drivers of Fish Spawning to Inform Environmental Flow Management." *Journal of Applied Ecology* 53: 34–43. <https://doi.org/10.1111/1365-2664.12542>.

- King, A. J., Z. Tonkin, and J. Lieshcke. 2012. "Short-Term Effects of a Prolonged Blackwater Event on Aquatic Fauna in the Murray River, Australia: Considerations for Future Events." *Marine and Freshwater Research* 63: 576–586. <https://doi.org/10.1071/MF11275>.
- Kirkpatrick, M., and N. H. Barton. 1997. "Evolution of a Species' Range." *American Naturalist* 150: 1–23. <https://doi.org/10.1086/286054>.
- Koehn, J. D., S. M. Raymond, I. Stuart, et al. 2020. "A Compendium of Ecological Knowledge for Restoration of Freshwater Fishes in Australia's Murray–Darling Basin." *Marine and Freshwater Research* 71: 1391–1463. <https://doi.org/10.1071/MF20127>.
- Kopelman, N. M., J. Mayzel, M. Jakobsson, N. A. Rosenberg, and I. Mayrose. 2015. "CLUMPAK: A Program for Identifying Clustering Modes and Packaging Population Structure Inferences Across K." *Molecular Ecology Resources* 15: 1179–1191. <https://doi.org/10.1111/1755-0998.12387>.
- Koster, W. M., D. R. Dawson, C. Liu, P. D. Moloney, D. A. Crook, and J. R. Thomson. 2017. "Influence of Streamflow on Spawning-Related Movements of Golden Perch *Macquaria ambigua* in South-Eastern Australia." *Journal of Fish Biology* 90: 93–108. <https://doi.org/10.1111/jfb.13160>.
- Leblanc, M., S. Tweed, A. Van Dijk, and B. Timbal. 2012. "A Review of Historic and Future Hydrological Changes in the Murray–Darling Basin." *Global and Planetary Change* 80–81: 226–246. <https://doi.org/10.1016/j.gloplacha.2011.10.012>.
- Leigh, C., F. Sheldon, R. T. Kingsford, and A. H. Arthington. 2010. "Sequential Floods Drive Booms and Wetland Persistence in Dryland Rivers: A Synthesis." *Marine and Freshwater Research* 61: 896–908. <https://doi.org/10.1071/MF10106>.
- Lesica, P., and F. W. Allendorf. 1995. "When Are Peripheral Populations Valuable for Conservation?" *Conservation Biology* 9: 753–760. <https://doi.org/10.1046/j.1523-1739.1995.09040753.x>.
- Lintermans, M. 2023. *Fishes of the Murray–Darling Basin*. 2nd ed. Canberra, ACT: Australian River Restoration Centre.
- Lotterhos, K. E. 2024. "Interpretation Issues With "Genomic Vulnerability" Arise From Conceptual Issues in Local Adaptation and Maladaptation." *Evolution Letters* 4: 331–339. <https://doi.org/10.1093/evlett/qrae004>.
- Layton, K. K. S., and I. R. Bradbury. 2021. "Harnessing the Power of Multi-omics Data for Predicting Climate Change Response." *Journal of Animal Ecology* 91: 1064–1072. <https://doi.org/10.1111/1365-2656.13619>.
- Mallen-Cooper, M., and B. P. Zampatti. 2018. "History, Hydrology and Hydraulics: Rethinking the Ecological Management of Large Rivers." *Ecohydrology* 11: e1965. <https://doi.org/10.1002/eco.1965>.
- Mallen-Cooper, M., and B. P. Zampatti. 2020. "Restoring the Ecological Integrity of a Dryland River: Why Low Flows in the Barwon–Darling River Must Flow." *Ecological Management & Restoration* 21: 218–228. <https://doi.org/10.1111/emr.12428>.
- Marshall, J. C., N. Menke, D. A. Crook, et al. 2016. "Go With the Flow: The Movement Behaviour of Fish From Isolated Waterhole Refugia During Connecting Flow Events in an Intermittent Dryland River." *Freshwater Biology* 61: 1242–1258. <https://doi.org/10.1111/fwb.12707>.
- McMahon, T. A., R. M. Vogel, M. C. Peel, and G. G. S. Pegram. 2007. "Global Streamflows — Part 1: Characteristics of Annual Streamflows." *Journal of Hydrology* 347: 243–259. <https://doi.org/10.1016/j.jhydrol.2007.09.002>.
- Moritz, C., and R. Agudo. 2013. "The Future of Species Under Climate Change: Resilience or Decline?" *Science* 341: 504–508. <https://doi.org/10.1126/science.1237190>.
- Muhlfeld, C. C., S. T. Kalinowski, T. E. McMahon, et al. 2009. "Hybridization Rapidly Reduces Fitness of a Native Trout in the Wild." *Biology Letters* 5: 328–331. <https://doi.org/10.1098/rsbl.2009.0033>.
- Murray–Darling Basin Authority. 2021. *The 2020 Basin Plan Evaluation: Social, Economic and Cultural Evidence Report*. Canberra, ACT: Murray–Darling Basin Authority.
- Musyl, M. K., and C. P. Keenan. 1992. "Population Genetics and Zoogeography of Australian Freshwater Golden Perch, *Macquaria ambigua* (Richardson 1845) (Teleostei: Percichthyidae), and Electrophoretic Identification of a New Species From the Lake Eyre Basin." *Marine and Freshwater Research* 43: 1585–1601. <https://doi.org/10.1071/MF9921585>.
- Nielsen, E. S., R. Henriques, M. Beger, and S. von der Heyden. 2021. "Distinct Interspecific and Intraspecific Vulnerability of Coastal Species to Global Change." *Global Change Biology* 27: 3415–3431. <https://doi.org/10.1111/gcb.15651>.
- Nixon, D., M. Hutchison, and A. Norris. 2022. "Golden Perch (*Macquaria ambigua*) in Refuge Waterholes in Ephemeral Rivers: The Effect of Town Proximity on Biomass and Size Structure." *Marine and Freshwater Research* 73: 1426–1438. <https://doi.org/10.1071/MF22074>.
- Nosil, P. 2012. *Ecological speciation*. Oxford, UK: Oxford University Press.
- Oksanen, J., G. Simpson, F. Blanchet, et al. 2022. "Vegan: Community Ecology Package." R Package Version 2.6-4. <https://CRAN.R-project.org/package=vegan>.
- Pavlova, A., K. A. Harrisson, R. Turakulov, et al. 2022. "Labile Sex Chromosomes in the Australian Freshwater Fish Family Percichthyidae." *Molecular Ecology Resources* 22: 1639–1655. <https://doi.org/10.1111/1755-0998.13569>.
- Pew, J., P. H. Muir, J. Wang, and T. R. Frasier. 2015. "Related: An R Package for Analysing Pairwise Relatedness From Codominant Molecular Markers." *Molecular Ecology Resources* 15: 557–561. <https://doi.org/10.1111/1755-0998.12323>.
- R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raj, A., M. Stephens, and J. K. Pritchard. 2014. "fastSTRUCTURE: Variational Inference of Population Structure in Large SNP Data Sets." *Genetics* 197: 573–589. <https://doi.org/10.1534/genetics.114.164350>.
- Razgour, O., B. Forester, J. B. Taggart, et al. 2019. "Considering Adaptive Genetic Variation in Climate Change Vulnerability Assessment Reduces Species Range Loss Projections." *Proceedings of the National Academy of Sciences, USA* 116: 10418–10423. <https://doi.org/10.1073/pnas.1820663116>.
- Rellstab, C., B. Dauphin, and M. Exposito-Alonso. 2021. "Prospects and Limitations of Genomic Offset in Conservation Management." *Evolutionary Applications* 14: 1202–1212. <https://doi.org/10.1111/eva.13205>.
- Reynolds, L. F. 1983. "Migration Patterns of Five Fish Species in the Murray–Darling River System." *Marine and Freshwater Research* 34: 857–871. <https://doi.org/10.1071/MF9830857>.
- Román-Palacios, C., and J. J. Wiens. 2020. "Recent Responses to Climate Change Reveal the Drivers of Species Extinction and Survival." *Proceedings of the National Academy of Sciences* 117: 4211–4217. <https://doi.org/10.1073/pnas.1913007117>.
- Sandoval-Castillo, J., K. Gates, C. J. Brauer, S. Smith, L. Bernatchez, and L. B. Beheregaray. 2020. "Adaptation of Plasticity to Projected Maximum Temperatures and Across Climatically Defined Bioregions." *Proceedings of the National Academy of Sciences* 117: 17112–17121. <https://doi.org/10.1073/pnas.1921124117>.
- Scheffers, B. R., L. De Meester, T. C. L. Bridge, et al. 2016. "The Broad Footprint of Climate Change From Genes to Biomes to People." *Science* 354: aaf7671. <https://doi.org/10.1126/science.aaf7671>.
- Schloss, C. A., T. A. Nuñez, and J. J. Lawler. 2012. "Dispersal Will Limit Ability of Mammals to Track Climate Change in the Western Hemisphere." *Proceedings of the National Academy of Sciences* 109: 8606–8611. <https://doi.org/10.1073/pnas.1116791109>.



- Schoeman, D. S., A. S. Gupta, C. S. Harrison, et al. 2023. "Demystifying Global Climate Models for Use in the Life Sciences." *Trends in Ecology & Evolution* 38: 843–858. <https://doi.org/10.1016/j.tree.2023.04.005>.
- Sheldon, F., D. Barma, L. J. Baumgartner, N. Bond, S. M. Mitrovic, and R. Vertessy. 2022. "Assessment of the Causes and Solutions to the Significant 2018–19 Fish Deaths in the Lower Darling River, New South Wales, Australia." *Marine and Freshwater Research* 73: 147–158. <https://doi.org/10.1071/MF21038>.
- Shelley, J. J., O. J. Holland, S. E. Swearer, et al. 2022. "Landscape Context and Dispersal Ability as Determinants of Population Genetic Structure in Freshwater Fishes." *Freshwater Biology* 67: 338–352. <https://doi.org/10.1111/fwb.13844>.
- Siepielski, A. M., M. B. Morrissey, M. Buoro, et al. 2017. "Precipitation Drives Global Variation in Natural Selection." *Science* 355: 959–962. <https://doi.org/10.1126/science.aag2773>.
- Smith, S., C. J. Brauer, M. Sasaki, et al. 2020. "Latitudinal Variation in Climate-Associated Genes Imperils Range Edge Populations." *Molecular Ecology* 29: 4337–4349. <https://doi.org/10.1111/mec.15637>.
- Stuart, I. G., and C. P. Sharpe. 2020. "Riverine Spawning, Long Distance Larval Drift, and Floodplain Recruitment of a Pelagophilic Fish: A Case Study of Golden Perch (*Macquaria ambigua*) in the Arid Darling River, Australia." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 675–690. <https://doi.org/10.1002/aqc.3311>.
- Sunnucks, P., and D. F. Hales. 1996. "Numerous Transposed Sequences of Mitochondrial Cytochrome Oxidase I-II in Aphids of the Genus *Sitobion* (Hemiptera: Aphididae)." *Molecular Biology and Evolution* 13: 510–524. <https://doi.org/10.1093/oxfordjournals.molbev.a025612>.
- Thacker, C. E., P. J. Unmack, L. Matsui, and N. Rifenburg. 2007. "Comparative Phylogeography of Five Sympatric *Hypseleotris* Species (Teleostei: Eleotridae) in South-Eastern Australia Reveals a Complex Pattern of Drainage Basin Exchanges With Little Congruence Across Species." *Journal of Biogeography* 34: 1518–1533. <https://doi.org/10.1111/j.1365-2699.2007.01711.x>.
- Thiem, J. D., L. J. Baumgartner, B. Fanson, A. Sadekov, Z. Tonkin, and B. P. Zampatti. 2022. "Contrasting Natal Origin and Movement History Informs Recovery Pathways for Three Lowland River Species Following a Mass Fish Kill." *Marine and Freshwater Research* 73: 237–246. <https://doi.org/10.1071/MF20349>.
- Tigano, A., and V. L. Friesen. 2016. "Genomics of Local Adaptation With Gene Flow." *Molecular Ecology* 25: 2144–2164. <https://doi.org/10.1111/mec.13606>.
- Tigano, A., T. Weir, H. G. M. Ward, et al. 2023. "Genomic Vulnerability of a Freshwater Salmonid Under Climate Change." *Evolutionary Applications* 17: e13602. <https://doi.org/10.1111/eva.13602>.
- Todesco, M., M. A. Pascual, G. L. Owens, et al. 2016. "Hybridization and Extinction." *Evolutionary Applications* 9: 892–908. <https://doi.org/10.1111/eva.12367>.
- Turbek, S. P., C. Bossu, C. Rayne, et al. 2023. "Historical DNA Reveals Climate Adaptation in an Endangered Songbird." *Nature Climate Change* 13: 735–741. <https://doi.org/10.1038/s41558-023-01696-3>.
- Unmack, P. J., B. D. Cook, J. B. Johnson, M. P. Hammer, and M. Adams. 2023. "Phylogeography of a Widespread Australian Freshwater Fish, Western Carp Gudgeon (Eleotridae: *Hypseleotris Klunzingeri*): Cryptic Species, Hybrid Zones, and Strong Intra-Specific Divergences." *Ecology and Evolution* 13: e10682. <https://doi.org/10.1002/ece3.10682>.
- Venables, W. N., and B. D. Ripley. 2002. *Modern Applied Statistics With S*. 4th ed. New York, NY: Springer.
- Voltaire, A., D. Saint-Martin, S. S en esi, et al. 2019. "Evaluation of CMIP6 DECK Experiments With CNRM-CM6-1." *Journal of Advances in Modeling Earth Systems* 11: 2177–2213. <https://doi.org/10.1029/2019MS001683>.
- Vranken, S., T. Wernberg, A. Scheben, et al. 2021. "Genotype–Environment Mismatch of Kelp Forests Under Climate Change." *Molecular Ecology* 30: 3730–3746. <https://doi.org/10.1111/mec.15993>.
- Walker, K. F. 2006. "Serial Weirs, Cumulative Effects: The Lower River Murray, Australia." In *The Ecology of Desert Rivers*, edited by R. T. Kingsford, 248–279. Cambridge, UK: Cambridge University Press.
- Wang, J. 2002. "An Estimator for Pairwise Relatedness Using Molecular Markers." *Genetics* 160: 1203–1215. <https://doi.org/10.1093/genetics/160.3.1203>.
- Weir, B. S., and C. C. Cockerham. 1984. "Estimating F-Statistics for the Analysis of Population Structure." *Evolution* 38: 1358–1370. <https://doi.org/10.2307/2408641>.
- Whetton, P., and F. Chiew. 2021. "Climate Change in the Murray-Darling Basin." In *Murray-Darling Basin, Australia: Its Future Management*, edited by B. T. Hart, N. R. Bond, N. Byron, C. A. Pollino, and M. J. Stewardson, vol. 1, 253–274. Amsterdam, the Netherlands: Elsevier.
- Whiteley, A. R., S. W. Fitzpatrick, W. C. Funk, and D. A. Tallmon. 2015. "Genetic Rescue to the Rescue." *Trends in Ecology & Evolution* 30: 42–49. <https://doi.org/10.1016/j.tree.2014.10.009>.
- Wiens, J. J. 2016. "Climate-Related Local Extinctions Are Already Widespread Among Plant and Animal Species." *PLoS Biology* 14: e2001104. <https://doi.org/10.1371/journal.pbio.2001104>.
- Wood, G., E. M. Marzinelli, A. H. Campbell, P. D. Steinberg, A. Verg es, and M. A. Coleman. 2021. "Genomic Vulnerability of a Dominant Seaweed Points to Future-Proofing Pathways for Australia's Underwater Forests." *Global Change Biology* 27: 2200–2212. <https://doi.org/10.1111/gcb.15534>.
- Wellenreuther, M., C. M erot, E. Berdan, and L. Bernatchez. 2019. "Going Beyond SNPs: The Role of Structural Genomic Variants in Adaptive Evolution and Species Diversification." *Molecular Ecology* 28: 1203–1209. <https://doi.org/10.1111/mec.15066>.
- Zampatti, B. P., S. J. Leigh, C. M. Bice, and P. J. Rogers. 2018. "Multiscale Movements of Golden Perch (Percichthyidae: *Macquaria ambigua*) in the River Murray, Australia." *Austral Ecology* 43: 763–774. <https://doi.org/10.1111/aec.12619>.

### Supporting Information

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