-

RESEARCH ARTICLE

Revised: 20 January 2022



Aridification-driven evolution of a migratory fish revealed by niche modelling and coalescence simulations

Emily J. Booth¹ | Jonathan Sandoval-Castillo¹ | Catherine R. M. Attard¹ | Dean M. Gilligan² | Peter J. Unmack³ | Luciano B. Beheregaray¹

¹Molecular Ecology Laboratory, College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia

²New South Wales Department of Primary Industries, Batemans Bay Fisheries Centre, Batemans Bay, New South Wales, Australia

³Centre for Applied Water Science, Institute for Applied Ecology, University of Canberra, Canberra, Australian Capital Territory, Australia

Correspondence

Luciano B. Beheregaray, Molecular Ecology Laboratory, College of Science and Engineering, Flinders University, Adelaide, SA 5001, Australia. Email: luciano.beheregaray@flinders.edu. au

Funding information Australian Research Council

Handling Editor: Camila Ribas

Abstract

Aim: Major knowledge gaps exist regarding the evolution of arid zone organisms. For freshwater species with high dispersal potential, little is known if historical aridification influenced connectivity across drainage divides and impacted on their divergence and diversification. We tested the hypothesis that the historical aridification of Australia promoted the isolation and influenced the demographic histories and evolutionary divergence of a migratory group of freshwater obligates.

Location: Central and eastern Australia; Murray–Darling Basin (MDB), Lake Eyre Basin (LEB), Fitzroy Basin (FIT).

Taxon: Three lineages of golden perch (*Macquaria ambigua*), a widespread fishery resource from inland Australia.

Methods: We obtained genome-wide data for golden perch sampled throughout their range. Phylogenetic relationships were reconstructed using maximum likelihood. Species distribution modelling was used to predict contemporary and past distributions for the three lineages and to develop hypotheses regarding their biogeographic and demographic histories. Hypotheses were independently tested using coalescent simulations in fastsimcoal and DIYABC with the genomic dataset.

Results: We found evidence for three reciprocally monophyletic lineages that have experienced little to nil genetic connectivity since divergence. Coalescent models suggest that the coastal (FIT) and inland (MDB and LEB) lineages diverged ~103 thousand years ago (ka), followed by the split of MDB and LEB lineages ~58 ka. These timings agree with reductions of large freshwater environments in Australia during the late Pleistocene. Species distribution models show an extreme decrease in habitat during the Last Glacial Maximum ~21 ka, consistent with inferred demographic contractions in coalescent tests.

Main conclusions: We reveal that aridification of Australia during the late Pleistocene has driven and reinforced the divergence of a migratory freshwater obligate. Our findings are important for informing the conservation management of aquatic organisms under climate change. This work further demonstrates the value of using species distribution modelling to formulate diversification hypotheses and to improve interpretation of coalescent analyses.

KEYWORDS

arid zone, climate change, freshwater fish, golden perch, historical biogeography, statistical phylogeography

1 | INTRODUCTION

Since the early 19th century, biogeographers have sought to understand the processes governing the spatial and temporal distributions of biodiversity (Avise, 2004). Despite the age of the discipline, some regions of the Earth, such as arid zones, remain particularly understudied (Beheregaray, 2008). The formation of widespread deserts and semi-arid landforms over the past several million years has caused major changes to global patterns of biodiversity (Brito et al., 2014; Martin, 2006). For example, the development of drier climatic niches has been linked to the adaptive radiation of various taxa including lizards and succulent plants (Arakaki et al., 2011; Carranza et al., 2008). In other cases, habitat fragmentation due to aridification has caused divergences through vicariance and by limiting species dispersal (Crisp & Cook, 2007; GonÇalves et al., 2018). Although studies are beginning to provide an insight into such processes, there are major knowledge gaps regarding the evolution of most arid zone taxa (Byrne et al., 2008). Increasing our understanding of the biogeographic and evolutionary history of arid zone species is relevant for managing wildlife under future climate change, which is expected to escalate drought severity and aridification in many parts of the world (Park et al., 2018).

The development of next generation sequencing has provided fast and affordable ways to produce large, multi-locus genomic datasets (McCormack et al., 2013). This has enhanced the use of coalescent modelling to statistically test competing theories regarding the demographic history of populations (Garrick et al., 2015). Coalescent analyses are based on 'coalescent theory', which presents a framework for simulating genealogies backwards in time—the power of this approach increasing with the number of genomic loci available (Rosenberg & Nordborg, 2002). Coalescent analyses require a priori hypotheses about the history of populations, such as effective sizes, divergence times or the timings and extent of bottlenecks (Cornuet et al., 2014; Excoffier et al., 2013). It is therefore important to combine coalescent analyses with other tools for developing such hypotheses.

Ecological niche modelling or species distribution modelling (SDM) is one approach that can be integrated with coalescent analyses (Gavin et al., 2014; Pahad et al., 2020). SDMs predictively map the geographic distribution of a species based on the relationship between known occurrence points of the species and environmental variables (Booth et al., 2014). These models can be projected onto historical or future environmental datasets (e.g. climate models) to map species distributions throughout time. Projecting species ranges backwards in geological time provides a way of developing historical biogeographic theories, which is especially important when empirical evidence such as fossils are lacking (Richards et al., 2007).

Australia provides an ideal setting for studying the evolutionary consequences of widespread aridification (Byrne et al., 2008). Today, arid and semi-arid biomes cover around 70% of the continent, however, conditions were once very different (Fujioka & Chappell, 2010). In the early Cenozoic, the continent was dominated by temperate rain forests and harboured expansive inland lakes (Martin, 2006). This changed during the late Miocene, when northward drift of the continent and global cooling caused the onset of major aridification around 14 million years ago (mya) (Fujioka & Chappell, 2010; Martin, 2006). Extensive alterations to hydrological regimes, vegetation cover and faunal assemblages accompanied this progressive aridification, including the contraction of rain forests and development of dry woodlands (Byrne et al., 2008; Martin, 2006). Throughout the Pleistocene, Australia endured phases of heightened aridity, interspersed with wetter periods, analogous to the glacial and interglacial cycles in the Northern Hemisphere (Byrne, 2008). Peak aridity and significant losses of surface water corresponded with the Last Glacial Maximum (LGM, ~21 ka) (De Deckker, 1986). These climate cycles led to genetic structuring in many taxa, as populations underwent a series of localised range contractions and expansions (Dolman & Joseph, 2016; Kireta et al., 2019; Pepper et al., 2011). While the evolution of Australia's terrestrial biota is becoming increasingly understood through biogeographic research, less is known about the influence of aridification on the divergence and persistence of aquatic species (Byrne et al., 2008).

Australian freshwater species often display deep phylogenetic structuring between drainage basins (Carini & Hughes, 2004; Hughes & Hillyer, 2003; Unmack, 2001). As freshwater organisms are generally unable to disperse across marine or terrestrial landscapes, their biogeographic histories are intrinsically linked to processes that alter the connectivity of freshwater habitats (Unmack, 2001). Reconfigurations of river networks can occur via a number of mechanisms, including stream capture, erosion and tectonic activity (Bishop, 1995). Australia has remained largely geologically stable since the Late Mesozoic, when the last major uplift of the Great Dividing Range occurred around 90 mya (Veevers, 1984). Drainage rearrangements caused by tectonic events are therefore unlikely to have influenced more recent evolutionary divergences (Unmack, 2001; but see Waters et al., 2019). Instead, reduced water connectivity across drainage divides intensified by aridification has potentially driven the isolation and divergence of many Australian freshwater species (Unmack, 2001).

Several studies have attempted to understand the timing of genetic divergences between populations from adjacent Australian drainage basins (Carini & Hughes, 2004; Faulks et al., 2015; Hughes et al., 2004; Unmack et al., 2019). These studies have revealed a lack of concordance among species, making it difficult to divulge largescale responses of aquatic biota to aridification (Thacker et al., 2007). Factors such as life history and dispersal ability are therefore considered to have played an important role in shaping the biogeography of freshwater taxa (Mossop et al., 2015). Additionally, molecular research has revealed that many Australian freshwater species exhibit cryptic diversity (Buckley et al., 2018; Unmack et al., 2017). Examining the evolution of cryptic lineages is crucial for clarifying taxonomy and informing conservation legislation (Beheregaray & Caccone, 2007). This is particularly true for our study species, golden perch (Macquaria ambigua).

Golden perch is an iconic Australian freshwater fish, distributed throughout much of the eastern semi-arid and central arid zones of the country. Its natural distribution spans three major drainage basins: the Murray-Darling (MDB), Lake Eyre (LEB) and Fitzroy (FIT); and the small sub-basin Bulloo-Bancannia (BULL) between the MDB and LEB (Figure 1). The species is of high cultural value, having contributed to the diet of indigenous Australians for over 20,000 years (Balme, 1995). This potamodromous medium-largesized fish is a popular target for recreational fishing, and is therefore regularly stocked from hatcheries into rivers and impoundments (Hunt & Jones, 2018). It is the most heavily stocked native fish in Australia, with over two million fingerlings released into the state of Victoria alone in 2020 (Victorian Fisheries Authority, 2020). Golden perch is a generalist species, with an opportunistic carnivorous diet and tolerance for a broad range of hydroclimatic conditions (Attard et al., 2018; Pusey et al., 2004). Golden perch are highly vagile during all life stages, and individuals have been reported to travel distances over 2000 km (Reynolds, 1983). The species responds to increased water temperature and flow during spring and summer by migrating upstream to spawn (Reynolds, 1983). This is believed to compensate for the subsequent downstream drift of their buoyant eggs and larvae (Pusey et al., 2004). Although populations of the species are generally well connected within each drainage basin (Faulks, Gilligan, & Beheregaray, 2010a, 2010b), landscape genomic analyses

Journal of Biogeography

point to adaptive divergence in subpopulations exposed to greater aridity and highly disturbed riverine flow (Attard et al., 2018). Due to their dependence on migration, the species is threatened by the development of dams and other anthropogenic actions such as climate change that disrupt river flow (Lintermans, 2007), particularly the loss of large flow events that initiate spawning and allow dispersal of small juveniles.

Golden perch are currently classified as a single, wide-ranging taxon (M. ambigua). However, several molecular studies have indicated that this might represent a species complex with substantial cryptic diversity (Beheregaray et al., 2017; Faulks et al., 2010a, 2010b; Musyl & Keenan, 1992). A recent analysis based on genomewide single nucleotide polymorphism (SNP) data proposed that there are three cryptic species, each endemic to a major drainage basin (FIT, LEB and MDB) (Beheregaray et al., 2017). Individuals from the BULL sub-basin were found to be admixed between LEB and MDB lineages, suggesting contemporary connectivity between these basins due to floods or human-mediated movement (Beheregaray et al., 2017). Clarifying the taxonomy of golden perch is vital for informing management practices and to prevent potential negative consequences of mixing different lineages, such as outbreeding depression and genetic swamping (Crook et al., 2016; Hindar et al., 1991) through intensive stocking. Current regulatory guidelines are in place to prevent this, however, translocations between basins have been relatively common in the past (Faulks et al., 2010a). Additionally, the recent detection of partially admixed individuals throughout the MDB suggests that deliberate illegal or accidental releases could still be occurring (Attard, Sandoval-Castillo, Gilligan, et al., 2022). As the taxonomy of golden perch remains unresolved, more research is needed to understand biogeographic processes underlying its cryptic diversity.

Here, we investigate the evolutionary history of golden perch using an integrative biogeographic framework. We first perform



FIGURE 1 Sampled localities from across the natural range of golden perch (*Macquaria ambigua*) in central and eastern Australia. Locality abbreviations are described in Table S1

4 ______ WILEY-_____Journal of Biogeogra

species distribution modelling to predict contemporary and historical distributions of golden perch. Resulting models are used to develop hypotheses about the demographic and biogeographic histories of the three major lineages. We then apply coalescent modelling based on genome-wide data to test competing hypotheses. Integrating these independent and complementary analyses is expected to provide a robust understanding of species history (Gavin et al., 2014; Kearns et al., 2014). Nonetheless, to the best of our knowledge such analytical integration is yet to be applied to freshwater organisms. This integrative framework is used here to (i) reconstruct the biogeographic history of the three major golden perch lineages, and (ii) elucidate the role that aridification has played on the divergence and maintenance of these lineages.

2 MATERIALS AND METHODS

2.1 Sampling, DNA extraction and ddRAD library preparation

We initially collected 603 golden perch from across the taxon's range using electrofishing and netting (Beheregaray et al., 2017; Faulks et al., 2010a, 2010b). From this total, a representative subset of 84 specimens were used to generate a double digestion restriction site associated DNA sequencing (ddRAD) dataset for a phylogenomics study (Beheregaray et al., 2017). Total DNA was extracted from caudal fin clips using a salting out protocol and ddRAD sequencing libraries were prepared and sequenced following Peterson et al. (2012) with modifications as in Brauer et al. (2016).

For the current study, we retained 62 of the 84 samples, encompassing 25 localities initially sampled throughout the Fitzroy, Lake Eyre and Murray-Darling basins (Figure 1, Table S1). These samples cover the geographic range of the three major golden perch lineages and their ecological envelopment. We excluded 20 highly admixed samples from the Bulloo-Bancannia Basin and the Dawson River, as their admixture (revealed by Beheregaray et al. (2017)) is thought to result from human-mediated gene flow. We also excluded two samples (one from MDB, one from LEB) with partial admixture with other basins that are considered an outcome of illegal or accidental mixing releases (Attard, Sandoval-Castillo, Gilligan, et al., 2022). Additionally, we retained eight samples from Beheregaray et al. (2017) that represent the two closest living relatives of golden perch, Macquarie perch (Macquaria australasica) and Bloomfield River cod (Guyu wujalwujalensis), which we used as outgroups for phylogenetics (Jerry et al., 2001).

2.2 **Bioinformatics**

Briefly, raw sequences were demultiplexed using 'process_radtags. pl' in the Stacks 1.19 pipeline (Catchen et al., 2013). Demultiplexed reads were trimmed to 84 bp, then processed using the pyRAD 3.0 pipeline (Eaton, 2014). All bases with a Phred quality score below 30 were replaced with N and reads with more than 4 Ns (5%) were discarded (Beheregaray et al., 2017). Filtered reads were clustered using a similarity threshold of 80%, and only clusters with $>10\times$ depth coverage per individual, <10% missing data and <0.6 observed heterozygosity were retained as loci (Beheregaray et al., 2017). We also removed individual samples with more than 20% missing data. Complete bioinformatics details are available from Beheregaray et al. (2017).

After this initial filtering, the remaining ddRAD loci were used for phylogenetic analyses in RAxML and IQ-TREE. For coalescent and TreeMix analyses, the sequence data were further filtered to remove outgroups and indels, and only include biallelic sites with a minor allele frequency $\geq 4\%$. We used an in-house script to extract one random SNP per ddRAD locus, and imputed missing data based on population allele frequencies using Genodive 3.04 (Meirmans, 2020).

2.3 **Phylogenetic analyses**

We reconstructed phylogenetic relationships between golden perch samples using a maximum likelihood (ML) approach. Initially, concatenated ddRAD sequences were used to produce a phylogenetic tree using RAxML 8.2.12 (Stamatakis, 2014). This analysis applied a general time-reversible substitution model with gamma-distributed rates among sites (GTR + GAMMA), and the best-scoring ML tree was found using rapid bootstrapping with 100 replicates. In addition, we implemented a partition model in IQ-TREE 2.0.3 (Nguyen et al., 2015) to account for rate heterogeneity among sites. For this analysis, sequences were partitioned by ddRAD loci. We inferred a ML species tree using an edge-proportional model, which allows each partition to evolve at an independent rate. Node support values were obtained from 1000 ultrafast bootstrap replicates (Hoang et al., 2017; Minh et al., 2020). We also estimated individual gene trees for each of the partitions using IQ-TREE. Gene and site concordance factors were subsequently calculated by comparing the gene trees to the species tree (Minh et al., 2020).

Tests for migration 2.4

We used TreeMix 1.13 (Pickrell & Pritchard, 2012) to assess connectivity or introgression events between the three golden perch lineages. TreeMix builds a maximum likelihood tree based on allele frequencies from a defined set of populations under a Gaussian approximation to genetic drift, then attempts to improve the likelihood by adding migration events (Pickrell & Pritchard, 2012). We constructed an unrooted ML tree, allowing for zero to three migration events. For this analysis we converted individual genotypes into population allele counts using 'populations' in the Stacks 2.4 pipeline (Catchen et al., 2013). To account for potential linkage

disequilibrium, SNPs were grouped in windows of 1000 sites for jackknife resampling.

2.5 | Species distribution modelling

Species distribution models were generated using the maximum entropy method implemented in Maxent 3.4.1 (Phillips et al., 2006). Maxent predicts the relative suitability of habitat across a landscape by modelling the relationship between presence-only species records and environmental variables. We estimated the contemporary distribution of golden perch lineages, then projected these models onto historical climatic layers to assess the influence of past aridification on their biogeography.

We obtained occurrence records of golden perch from the Atlas of Living Australia (www.ala.org.au). To group records by distinct lineages, we independently extracted occurrences from within the three major drainage basins (FIT, LEB and MDB) using the polygon tool. To minimise uneven sampling bias, occurrences were filtered to be at least 1 km apart using the R package 'spThin' (Aiello-Lammens et al., 2015). The final dataset included 1226 occurrence points (FIT, n = 75; LEB, n = 59; MDB, n = 1092).

Contemporary and historical bioclimatic variables were downloaded from PaleoClim (www.paleoclim.org) with 2.5 arc-minute resolution. This database contains 19 biologically meaningful variables derived from monthly temperature and rainfall values (Brown, Hill, Dolan, Carnaval, & Haywood, 2018). Although there are uncertainties in using terrestrial-based variables for freshwater SDMs, studies have shown that macro-scale variables can be appropriate proxies for local stream conditions and for patterns of aquatic adaptation (Frederico et al., 2014). Our historical environmental layers included variables estimated for Marine Isotope Stage 19 (MIS19, ~787 ka), the Last Interglacial (LIG, ~130 ka) and the Last Glacial Maximum (LGM, ~21 ka) (Brown et al., 2018; Karger et al., 2017; Otto-Bliesner et al., 2006). All bioclimatic variables were imported into ArcMap 10.6 and clipped to the spatial extent of Australia. A Pearson's correlation matrix was generated using the package 'stats 3.6' in R to evaluate correlations among the variables (Table S2). Strongly correlated variables (r > 0.8) were removed, selectively keeping uncorrelated variables that showed high discrimination importance in preliminary SDMs. As variables bio3 and bio6 were unavailable for MIS19, we also removed these. The final models were based on five bioclimatic variables: annual mean temperature (bio1), mean temperature of driest quarter (bio9), precipitation of driest month (bio14), precipitation seasonality (bio15) and precipitation of warmest quarter (bio18). Models were generated using default settings (linear, quadratic, product and hinge features; regularisation multiplier = 1) with 25% of occurrence points reserved for testing. Model performance was evaluated using the area under the curve (AUC) method. To test for reductions in range area across time, we converted SDMs to binary presence-absence maps. We considered presence as cell suitability ≥0.25, then calculated the number of putative presence cells for each lineage. Putative presence maps

were also used to estimate reductions in overlapping areas between lineages.

Journal of <u>Biogeog</u>raphy

2.6 | Coalescent modelling

Two coalescent-based modelling approaches were used to further estimate the phylogeographic and demographic histories of golden perch lineages. We primarily used fastsimcoal 2.6 (Excoffier et al., 2013; Excoffier & Foll, 2011), which performs coalescent simulations based on user-defined models and assesses model fitness by comparing results to an empirical allele frequency spectrum. This program allows for the testing of comprehensive models, including population size changes, migrations and divergence events (Excoffier et al., 2013). It has performed well in phylogeographic studies to infer complex evolutionary histories (Kautt et al., 2016). Our empirical dataset consisted of the joint minor-allele frequency spectrum (joint-MAF) for each pair of lineages.

We initially tested three phylogenetic scenarios to establish an underlying model of golden perch evolution (Table S3, Figure S1). Each of the three scenarios were tested under 'early' divergence time priors, which encompass dates previously estimated from mitochondrial DNA (Faulks et al., 2010a), and more 'recent' divergence times that were informed by our SDMs (Figure S1). We converted from number of generations to years by multiplying by eight (twice the age of maturity for female golden perch) (Pusey et al., 2004). We also repeated the above models, changing which lineage was considered the 'sink' deme (i.e. the one largely informing the ancestral population size) when lineages merged (Table S3). Results from these additional analyses are available in supplementary material. For all fastsimcoal models, we used a mutation rate of 2 \times 10⁻⁸ per generation per locus, following an example in the user manual (Excoffier, 2016). This mutation rate was used since there is no calibrated molecular clock for golden perch (Faulks et al., 2010a).

For the two best performing models, we ran additional tests that incorporated demographic contractions at the LGM and/or historical migration events. In total, 29 different coalescent models were tested, and for each we performed 100 independent runs of fastsimcoal (40 ECM cycles and 10,000 simulations per run) (Table S3). The run with the highest likelihood was selected to compare the fitness of each model based on Akaike's information criterion (AIC). For the overall top performing model, we calculated 95% confidence intervals of parameter estimates. This was done by simulating 1000 bootstrap MAF spectrums based on the maximum likelihood parameters estimated in the previous step, then re-estimating the parameters by performing 20 runs of the top performing model for each simulated dataset. Confidence intervals were obtained using the R function boot.ci from the package 'boot 1.3'.

In addition to fastsimcoal, we assessed the three phylogenetic scenarios under 'recent' divergence times using DIYABC 2.1.4 (Cornuet et al., 2014). DIYABC is a coalescent-based program that implements approximate Bayesian computation. For each of the

three models, we simulated 6,000,000 SNP datasets. The posterior probability of each model was measured as the relative proportion of each model in the simulated datasets closest to the observed dataset. Similarity was measured through the Euclidian distance between normalised simulated and observed summary statistics.

RESULTS 3

Sequence characteristics 3.1

Bioinformatic analyses produced high-quality data for 70 samples (includes the eight outgroups) (Table S1). For phylogenetics, the novel concatenated dataset consisted of ~2.026 million bp from 24,051 ddRAD loci with 134,107 variable and 100,967 parsimony informative sites present in >90% of individuals. After further filtering, 7103 putatively unlinked biallelic SNPs (from the same number of ddRAD loci) were retained for coalescent and TreeMix analyses. For this unlinked SNP dataset, missing data (<3% average per site and individual) were imputed.

3.2 Phylogenetic analyses and tests for migration

Our concatenated and partitioned ML analyses revealed three reciprocally monophyletic clades, each consisting of individuals sampled from one of the three major drainage basins. This was supported by 100% bootstrap and high (>95%) site concordance factors (SCFs) in the IQ-TREE analysis (Figure 2a, Figures S2–S3). Gene concordance factors (GCFs) were low, although this is to be expected for trees with short branch lengths (Minh et al., 2020) and short read sequences (Rivers et al., 2016). The phylogenetic reconstruction identified an initial split between the coastal (FIT) and inland (LEB and MDB) basins, followed by divergence of the LEB and MDB clades. Within the

LEB we found strong support (100% bootstrap, Figure 2a) for two sub-clades, one comprising samples from the eastern catchment (Cooper, Barcoo, and Thomson) and the other comprising western catchment samples (Diamantina, Georgina, Neales, and Warburton). Little genetic structuring was identified within the MDB, although some samples from the same locality tended to cluster together, such as in the Lower Lakes. Our TreeMix analysis found no support for migration between any of the three identified clades (Figure 2b).

Species distribution modelling 3.3

All our Maxent models have high predictive power with both training and test datasets exhibiting AUC > 0.90 (Figure S4). Final models included five bioclimatic variables: annual mean temperature (bio1), mean temperature of driest quarter (bio9), precipitation of driest month (bio14), precipitation seasonality (bio15) and precipitation of warmest guarter (bio18). Based on jackknife tests, all five variables contributed considerably to each model (Table S4, Figure S5). Contemporary predicted ranges are broadly consistent with known distributions; however, they indicate additional suitable habitat in south-western Western Australia for the MDB lineage and an extended westward distribution for the LEB lineage (Figure 3d). Under the current climate, models show a low degree of overlap between the lineages in the east of the country, indicating the potential for some connectivity (Figure 3d, Figures S6-S7). Projected SDMs for MIS19 (~787 ka), a previous interglacial period, are generally alike the contemporary models but with less suitable habitat along the eastern coast (Figure 3a, Figures S6-S7). SDMs for the LIG (~130 ka) predict a remarkably smaller amount of habitat for the LEB and FIT lineages compared to today, but also some distributional overlap with possible connectivity among all three lineages (Figure 3b, Figures S6-S7). SDMs for the LGM (~21 ka) indicate that suitable habitat was substantially reduced



FIGURE 2 (a) Maximum likelihood phylogeny of golden perch (Macquaria ambigua) based on ~2.026 million bp of ddRAD sequences, partitioned into 24,051 loci, Three reciprocally monophyletic lineages are represented by samples from the Fitzroy (FIT), Murray–Darling (MDB) and Lake Eyre (LEB) basins. All major clades are supported by 100% bootstrap, as denoted by asterisks. Macquarie perch (Macquaria australasica, abbreviated as MP) and Bloomfield River cod (Guyu wujalwujalensis, abbreviated as GW) were used as outgroups. (b) Unrooted maximum likelihood tree inferred with TreeMix based on 7103 SNPs; no migration events are supported between lineages



Journal of Biogeography -WILEY^{___7}

FIGURE 3 Species distribution models for three golden perch (*Macquaria ambigua*) lineages, projected for: (a) Marine Isotope Stage 19 (~787 ka), (b) Last Interglacial (~130 ka), (c) Last Glacial Maximum (~21 ka), (d) present day. Each lineage is currently endemic to one of three major Australian drainage basins: Fitzroy (FIT), Lake Eyre (LEB), Murray–Darling (MDB). Colour tone indicates habitat suitability for each lineage

for all lineages, which could suggest major reductions in population size and stronger isolation between the drainages during that time (Figure 3c, Figures S6–S7).

3.4 | Coalescent modelling

Our fastsimcoal analyses revealed that all three evolutionary models performed better under the more recent divergence time priors (i.e. when all lineages coalesce within the past 120 thousand years). Under these divergence times, models 1 and 3 had the lowest AIC scores (Table S3) and were therefore selected as the basis for further model developments. The overall top performing model was based on model 1 and incorporated a halving of effective population sizes near the LGM (looking backwards in time) with no migration between lineages (Figure 4). This model is also supported by the SDMs, which show a decrease in suitable habitat at the LGM, and the TreeMix analysis, which indicates no historical migration between lineages. Maximum likelihood parameter estimates and confidence intervals, along with the priors for the best performing model are detailed in Table 1.

DIYABC found highest support for model 1 (where LEB and MDB are sister lineages), although the posterior probabilities for all models were low (<0.4) (Figure S8–S9). This suggests that model 1, which was also supported by fastsimcoal and the ML phylogenetic reconstruction, represents the most likely scenario for the divergence of the three golden perch lineages.

4 | DISCUSSION

Understanding how past climatic changes have influenced range limits, population demography and evolutionary diversification is a long-standing goal of biogeography. This is particularly important for poorly studied biotas from arid and semi-arid zones, which are projected to be severely impacted by anthropogenic climate change (Park et al., 2018). We combined coalescent analyses based on genome-wide data and species distribution modelling to investigate the biogeographic and evolutionary history of golden perch (*Macquaria ambigua*), a migratory freshwater obligate with a vast range in arid and semi-arid regions of Australia. Our integrative framework provides support for the previously proposed delimitation of three cryptic species, each endemic to one of the three major drainage basins where golden perch is naturally found: the Murray-Darling, Lake Eyre and Fitzroy. The results indicate that



FIGURE 4 Schematic of the most strongly supported fastsimcoal coalescent model for the evolutionary history of golden perch (*Macquaria ambigua*) lineages. FIT: Fitzroy Basin, LEB: Lake Eyre Basin, MDB: Murray–Darling Basin. This model incorporates a halving of effective population size for each lineage (looking backwards in time) at the dates indicated in Table 1

major demographic and evolutionary events of this species complex occurred during the late Pleistocene, in agreement with the hypothesis that historical aridification of Australia promoted the isolation and divergence of freshwater taxa.

This is the first study to statistically assess competing scenarios of evolutionary divergence in this widespread and socio-economically important migratory species with a combination of genomics and species distribution modelling. We further demonstrate the benefits of integrating genomic and environmental datasets to improve the development and testing of biogeographic hypotheses.

4.1 | The role of aridification in evolutionary diversification

Throughout the Pleistocene epoch (2.6 mya to 11.7 ka), Earth experienced a series of climatic oscillations between glacial and interglacial conditions (Paillard, 2006). These manifested in Australia as phases of heightened aridity interspersed with the formation of broader wetlands (Martin, 2006). During the moist interglacials, the low topographic relief of Australia allowed for frequent connections of drainage basins (Unmack, 2001). In contrast, intense desiccation during glacial periods enhanced drainage divides and caused the overall fragmentation of freshwater habitats, leading to evolutionary divergences. This has been inferred by strong population genetic structuring in many widespread aquatic taxa, including prawns (Carini & Hughes, 2004), crayfish (Hughes & Hillyer, 2003), and teleosts (Beheregaray et al., 2017; Jerry, 2008; Unmack, 2001).

Our results indicate that the coastal (FIT) and inland (MDB and LEB) lineages of golden perch diverged ~103 ka, followed by separation of the MDB and LEB lineages ~58 ka (Table 1). These divergence dates fall within a time period when there was a general trend towards reduced water connectivity of large freshwater lakes in central

Australia (Cohen et al., 2015; Fu et al., 2017). For instance, since a peak highstand ~125 ka the Lake Eyre playa has decreased in size by approximately three times (DeVogel et al., 2004). We propose that during wetter phases the strong vagility and broad ecological tolerance of golden perch has facilitated movement between drainage basins, maintaining genetic connectivity until the onset of extreme aridification. This inference is supported by our SDMs, which suggest that the three lineages were well connected during previous interglacial periods (Figure 3). Our SDMs also indicate large reductions in suitable habitat during the LGM (Figure 3), with the results of coalescent testing supporting demographic expansions after the LGM (Table 1, Figure 4). Earlier research based on mitochondrial DNA also recovered signals of historical demographic expansions in the MDB and LEB lineages (Faulks et al., 2010a). These expansions were previously suggested to have occurred ~220 ka and ~170 ka respectively (Faulks et al., 2010a). Although these dates are earlier than our coalescent models suggest, some discrepancies are expected due to the lack of a calibrated molecular clock for golden perch (Faulks et al., 2010a) and the better sampling of demographic histories and multiple gene trees provided by the genomic data compared to the single locus tree sampled by the mitochondrial genome (Garrick et al., 2015). Nevertheless, there was concordance in the general pattern disclosed by the two different genetic datasets (mitochondrial DNA and SNPs) and independent environmental reconstructions (SDMs).

4.2 | Integration of coalescent and species distribution modelling

Biogeographic research is often challenging because it aims to infer past events that cannot be directly observed (Kidd & Ritchie, 2006). While coalescent modelling provides a way to assess historical population processes, it also relies on the development of testable hypotheses (Richards et al., 2007). Such hypotheses are often conceived based on inferences about how climatic fluctuations have influenced the size and connectivity of populations (Chattopadhyay et al., 2017). However, few studies have used species distribution modelling to inform or corroborate coalescent analyses (de Melo et al., 2016; Gavin et al., 2014; Kearns et al., 2014). This is surprising, given the relative ease of acquiring environmental and species occurrence data from publicly available databases (Richards et al., 2007). The benefits of combining coalescent analyses and SDMs have been exemplified by Kearns et al. (2014) in a study on Australian butcherbirds. In their study, SDMs indicated that the arid-adapted grey butcherbird (Cracticus torquatus) had a larger range during the LGM compared to the present day. This inference was supported by coalescent modelling, which proposed a population expansion and secondary contact with a closely related species during the same time (Kearns et al., 2014).

Seeking agreement between these independent approaches is valuable, as each can be prone to inaccuracies and over-interpretation (Richards et al., 2007). As aforementioned, our SDMs indicate extreme reductions in habitat for golden perch during the LGM (Figure 3). This

ournal of Biogeography

TABLE 1 Maximum likelihood parameter estimates for the best performing fastsimcoal coalescent model for the evolution of golden perch (Macquaria ambigua) lineages

Parameter		Point estimate	Confidence interval (95%)	Prior
Effective population size (Ne)	FIT (current)	1155	729-1243	100-10,000
	LEB (current)	1196	972-1886	100-10,000
	MDB (current)	1861	1535-2836	100-100,000
Divergence time (ya)	LEB from MDB	58,032	25,144-65,616	20,000-70,000
	Ancestral MDB/LEB from FIT	103,208	74,944-116,768	70,000-120,000
Population reduction time ^a (ya)	FIT	16,696	10,896-18,752	10,000-18,000
	LEB	11,616	9912-19,096	10,000-18,000
	MDB	12,088	10,424-19,064	10,000-18,000

Abbreviations: FIT, Fitzroy Basin; LEB, Lake Eyre Basin; MDB, Murray-Darling Basin; ya, years ago.

^aTime when each lineage experienced a halving of effective population size (looking backwards in time).

is especially true for the FIT and LEB lineages, which have no areas of predicted habitat in Australia. However, literature on the sedimentary history of the Fitzroy and Lake Eyre basins reveal localised episodes of fluvial activity around the LGM (Croke et al., 2011; Nanson et al., 2008). It is therefore probable that these lineages persisted in reduced areas during this period but had a broader distribution than suggested by the SDMs. A modified figure that considers the presence of water at the LGM is provided in supplementary material (Figure S10). We recognise that the lack of water data for historical drainages limits the inference about historical distribution and physical connectivity of freshwater fish populations. Nevertheless, approaches that incorporate data from regional climate models (e.g. Attard, Sandoval-Castillo, Brauer, et al., 2022; Buckley et al., 2021) can produce reasonable hypotheses to be tested through a coalescent framework at a basin and lineage level, as demonstrated here.

4.3 | Future directions and implications for conservation management under climate change

This study highlights the need for improved biological sampling and scientific research in arid regions of the world. We found that the number of golden perch records available for the arid Lake Eyre Basin was much lower than for the more temperate Murray-Darling Basin (59 compared to 1092 after filtering). This may have impacted the development of our SDMs, particularly when projecting the models to historical times. However, we note that occurrence records were spaced throughout the LEB, capturing the broad bioclimatic envelope of the lineage. An increased focus on arid biomes, and especially their freshwater elements, is important for understanding how to manage them under future environmental change (Byrne, 2008). Freshwater ecosystems are severely threatened on a global scale due a multitude of factors such as habitat degradation, pollution and water extraction (Williams-Subiza & Epele, 2021). In arid settings, these stresses are exacerbated by the natural isolation of water bodies (Attard, Sandoval-Castillo, Brauer, et al., 2022; Murphy et al., 2015). The Australian arid zone contains various types of freshwater habitats, ranging from ephemeral rivers

and isolated waterholes to permanent groundwater-fed springs (Fensham et al., 2011). These systems are often connected during high rainfall events, facilitating organismal dispersal between localities (Attard, Sandoval-Castillo, Brauer, et al., 2022; Fensham et al., 2011). Anthropogenic climate change is projected to increase aridity over much of Australia in coming decades, leading to more variable flow regimes and declines in water connectivity (Larkin et al., 2020). Our study demonstrates how such fragmentation of freshwater habitats can minimise or prevent gene flow between isolated lineages. Although golden perch currently show low genetic differentiation within each drainage basin (Faulks et al., 2010a, 2010b), climate change could disrupt population connectivity in future. Maintaining genetic connectivity between populations within distinct lineages is often vital for ensuring their long-term persistence, especially under climate change (Frankham et al., 2019).

Golden perch in the arid reaches of the MDB have been found to exhibit adaptive genetic diversity linked to functions such as fat storage, which allows them to survive severely dry periods (Attard et al., 2018). Contemporary connectivity of golden perch throughout the MDB is expected to facilitate the spread of these adaptive traits, which could become selected for in other regions as environmental conditions change (Attard et al., 2018). It is therefore important to focus conservation efforts on maintaining the connectivity of habitats (within drainage basins), for example through the construction of fish passages (Baumgartner et al., 2014). This will maximise the sharing of beneficial genetic variation that may be necessary for populations to survive extreme events such as heat waves and droughts that are expected to occur more frequently in future (Leigh et al., 2015).

Our work adds to several existing studies that have identified cryptic diversity within *M. ambigua* based on allozymes and morphology (Musyl & Keenan, 1992), mitochondrial DNA (Faulks et al., 2010a), microsatellites (Faulks et al., 2010b) and SNP data (Beheregaray et al., 2017). Our more advanced phylogenetic and coalescent analyses support the proposition that lineages from the Murray-Darling, Lake Eyre and Fitzroy drainage basins should be considered as separate species (Beheregaray et al., 2017). Our TreeMix and coalescent analyses found little evidence of gene flow since the lineages diverged. We recommend that stocking WILEY^{_} Journal of Biogeography

and translocations of golden perch do not take place between drainage basins. Although this is currently regulated, there is evidence that some illegal or unintentional releases may still be occurring (Attard, Sandoval-Castillo, Gilligan, et al., 2022). Stocked individuals contribute to the genetic diversity of golden perch and could potentially swamp natural populations (Crook et al., 2016).

ACKNOWLEDGEMENTS

This project was funded by an Australian Research Council Future Fellowship (FT130101068 to L. B. B.) and sampling was made under permits from various state fisheries agencies and under Flinders University Animal Welfare Committee approvals E313 and E342. We thank Lauren Pfeiffer for lab support and the researchers that provided tissue samples or participated in our field expeditions, including Leanne Faulks, Michael Hammer, Mark Adams, Rupert Mathwin, David Cheshire, David Schmarr, Dale McNeil, Gabriel Shepherd, David Sternberg, Kim Shaddick and Julien April. This work received logistic support from Flinders University, Macquarie University, University of Canberra, South Australian Museum, NSW Department of Primary Industries, Department of Environment, Water and Natural Resources SA, South Australian Research and Development Institute, Department of Natural Resources and Mines QLD.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://figshare.com/, reference number https:// figshare.com/s/65774d60e6f9f0b3031b.

ORCID

Jonathan Sandoval-Castillo 💿 https://orcid. org/0000-0002-8428-3495

Luciano B. Beheregaray 🕩 https://orcid.org/0000-0003-0944-3003

REFERENCES

- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38(5), 541–545.
- Arakaki, M., Christin, P., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R. M., Spriggs, E., Moore, M. J., & Edwards, E. J. (2011). Contemporaneous and recent radiations of the world's major succulent plant lineages. Proceedings of the National Academy of Sciences of the United States of America, 108(20), 8379–8384. https://doi.org/10.1073/ pnas.1100628108
- Attard, C. R. M., Brauer, C. J., Sandoval-Castillo, J., Faulks, L. K., Unmack, P. J., Gilligan, D. M., & Beheregaray, L. B. (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(1), 196–215.
- Attard, C. R. M., Sandoval-Castillo, J., Brauer, C., Unmack, P. J., Schmarr, D., Bernatchez, L., & Beheregaray, L. B. (2022). Fish out of water:

Genomic insights into persistence of rainbowfish populations in the desert. *Evolution*, *76*, 171–183.

- Attard, C. R. M., Sandoval-Castillo, J., Gilligan, D. M., Unmack, P. J., Faulks, L. K., Beheregaray, L. B. (2022). Genomics outperforms genetics to manage mistakes in fisheries stocking of threatened species. *Biodiversity and Conservation*. https://doi.org/10.1007/ s10531-022-02369-x
- Avise, J. C. (2004). What is the field of biogeography, and where is it going? *Taxon*, *53*(4), 893–898.
- Balme, J. (1995). 30,000 years of fishery in western New South Wales. Archaeology in Oceania, 30(1), 1–21.
- Baumgartner, L., Zampatti, B., Jones, M., Stuart, I., & Mallen-Cooper, M. (2014). Fish passage in the Murray-Darling basin, Australia: Not just an upstream battle. *Ecological Management and Restoration*, 15, 28–39.
- Beheregaray, L. B. (2008). Twenty years of phylogeography: The state of the field and the challenges for the southern hemisphere. *Molecular Ecology*, 17, 3754–3774.
- Beheregaray, L. B., & Caccone, A. (2007). Cryptic biodiversity in a changing world. *Journal of Biology*, 6(4), 9.
- Beheregaray, L. B., Pfeiffer, L. V., Attard, C. R. M., Sandoval-Castillo, J., Domingos, F. M. C. B., Faulks, L. K., Gilligan, D. M., & Unmack, P. J. (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
- Bishop, P. (1995). Drainage rearrangement by river capture, beheading and diversion. Progress in Physical Geography, 19(4), 449–473.
- Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). Bioclim: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, 20, 1–9.
- Brauer, C. J., Hammer, M. P., & Beheregaray, L. B. (2016). Riverscape genomics of a threatened fish across a hydroclimatically heterogeneous river basin. *Molecular Ecology*, 25(20), 5093–5113.
- Brito, J. C., Godinho, R., Martínez-Freiría, F., Pleguezuelos, J. M., Rebelo, H., Santos, X., Vale, C. G., Velo-Antón, G., Boratyński, Z., Carvalho, S. B., Ferreira, S., Gonçalves, D. V., Silva, T. L., Tarroso, P., Campos, J. C., Leite, J. V., Nogueira, J., Álvares, F., Sillero, N., & Carranza, S. (2014). Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biological Reviews*, *89*(1), 215–231. https:// doi.org/10.1111/brv.12049
- Brown, J. L., Hill, D. J., Dolan, A. M., Carnaval, A. C., & Haywood, A. M. (2018). PaleoClim, high spatial resolution paleoclimate surfaces for global land areas. *Scientific Data*, 5(1), 180254.
- Buckley, S. J., Brauer, C. J., Unmack, P. J., Hammer, M. P., & Beheregaray, L. B. (2021). The roles of aridification and sea level changes in the diversification and persistence of freshwater fish lineages. *Molecular Ecology*, 30, 4866–4883.
- Buckley, S. J., Domingos, F. M. C. B., Attard, C. R. M., Brauer, C. J., Sandoval-Castillo, J., Lodge, R., Unmack, P. J., & Beheregaray, L. B. (2018).
 Phylogenomic history of enigmatic pygmy perches: Implications for biogeography, taxonomy and conservation. *Royal Society Open Science*, 5(6), 172125. https://doi.org/10.1098/rsos.172125
- Byrne, M. (2008). Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. *Quaternary Science Reviews*, 27(27), 2576–2585.
- Byrne, M., Yeates, D. K., Joseph, L., Kearney, M., Bowler, J., Williams, M. A. J., Cooper, S., Donnellan, S. C., Keogh, J. S., Leys, R., Melville, J., Murphy, D. J., Porch, N., & Wyrwoll, K.-H. (2008). Birth of a biome: Insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, 17, 4398–4417. https://doi. org/10.1111/j.1365-294X.2008.03899.x
- Carini, G., & Hughes, J. M. (2004). Population structure of *Macrobrachium australiense* (Decapoda: Palaemonidae) in Western Queensland,

Australia: The role of contemporary and historical processes. *Heredity*, 93(4), 350–363.

- Carranza, S., Arnold, E. N., Geniez, P., Roca, J., & Mateo, J. A. (2008). Radiation, multiple dispersal and parallelism in the skinks, *Chalcides* and *Sphenops* (Squamata: Scincidae), with comments on *Scincus* and *Scincopus* and the age of the Sahara Desert. *Molecular Phylogenetics* and Evolution, 46(3), 1071–1094.
- Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An analysis tool set for population genomics. *Molecular Ecology*, 22(11), 3124–3140.
- Chattopadhyay, B., Garg, K. M., Gwee, C. Y., Edwards, S. V., & Rheindt, F. E. (2017). Gene flow during glacial habitat shifts facilitates character displacement in a neotropical flycatcher radiation. BMC Evolutionary Biology, 17(1), 210.
- Cohen, T., Jansen, J., Gliganic, L., Larsen, J., Nanson, G., May, J.-H., Jones, B., & Price, D. (2015). Hydrological transformation coincided with megafaunal extinction in Central Australia. *Geology*, 43(3), 195– 198. https://doi.org/10.1130/G36346.1
- Cornuet, J.-M., Pudlo, P., Veyssier, J., Dehne-Garcia, A., Gautier, M., Leblois, R., Marin, J.-M., & Estoup, A. (2014). DIYABC v2. 0: A software to make approximate Bayesian computation inferences about population history using single nucleotide polymorphism, DNA sequence and microsatellite data. *Bioinformatics*, 30(8), 1187-1189.
- Crisp, M. D., & Cook, L. G. (2007). A congruent molecular signature of vicariance across multiple plant lineages. *Molecular Phylogenetics and Evolution*, 43(3), 1106–1117.
- Croke, J., Jansen, J. D., Amos, K., & Pietsch, T. J. (2011). A 100 ka record of fluvial activity in the Fitzroy River basin, tropical northeastern Australia. *Quaternary Science Reviews*, 30(13), 1681–1695.
- Crook, D. A., Mahony, D. J., Gillanders, B. M., Munro, A. R., Sanger, A. C., Thurstan, S., & Baumgartner, L. J. (2016). Contribution of stocked fish to riverine populations of golden perch (*Macquaria ambigua*) in the Murray-Darling basin, Australia. *Marine and Freshwater Research*, 67(10), 1401–1409.
- De Deckker, P. (1986). What happened to the Australian aquatic biota 18000 years ago? In P. De Deckker & W. D. Williams (Eds.), *Limnology in Australia* (Vol. 61, pp. 487–496). Springer Science & Business Media.
- de Melo, W. A., Lima-Ribeiro, M. S., Terribile, L. C., & Collevatti, R. G. (2016). Coalescent simulation and paleodistribution modeling for *tabebuia rosealba* do not support south American dry forest refugia hypothesis. *PLoS One*, 11(7), e0159314.
- DeVogel, S. B., Magee, J. W., Manley, W. F., & Miller, G. H. (2004). A GIS-based reconstruction of late quaternary paleohydrology: Lake Eyre, arid Central Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 204(1), 1–13.
- Dolman, G., & Joseph, L. (2016). Multi-locus sequence data illuminate demographic drivers of Pleistocene speciation in semi-arid southern Australian birds (*Cinclosoma* spp.). BMC Evolutionary Biology, 16, 226.
- Eaton, D. A. R. (2014). PyRAD: Assembly of de novo RADseq loci for phylogenetic analyses. *Bioinformatics*, 30(13), 1844–1849.
- Excoffier, L. (2016). fsc26 manual. Retrieved from http://cmpg.unibe.ch/ software/fastsimcoal26/man/fastsimcoal26.pdf
- Excoffier, L., Dupanloup, I., Huerta-Sánchez, E., Sousa, V. C., & Foll, M. (2013). Robust demographic inference from genomic and SNP data. *PLoS Genetics*, 9(10), e1003905.
- Excoffier, L., & Foll, M. (2011). Fastsimcoal: A continuous-time coalescent simulator of genomic diversity under arbitrarily complex evolutionary scenarios. *Bioinformatics*, 27(9), 1332–1334.
- Faulks, L. K., Gilligan, D., & Beheregaray, L. B. (2015). "Ragged mountain ranges, droughts and flooding rains": The evolutionary history and conservation of Australian freshwater fishes. In A. Stow, N. Mclean, & G. Holwell (Eds.), *Austral ark*. Cambridge University Press.

Faulks, L. K., Gilligan, D. M., & Beheregaray, L. B. (2010a). Clarifying an ambiguous evolutionary history: Range-wide phylogeography of an Australian freshwater fish, the golden perch (*Macquaria ambigua*). *Journal of Biogeography*, 37(7), 1329–1340.

geography

- Faulks, L. K., Gilligan, D. M., & Beheregaray, L. B. (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(21), 4723–4737.
- Fensham, R. J., Silcock, J. L., Kerezsy, A., & Ponder, W. (2011). Four desert waters: Setting arid zone wetland conservation priorities through understanding patterns of endemism. *Biological Conservation*, 144(10), 2459–2467.
- Frankham, R., Ballou, J. D., Ralls, K., Eldridge, M., Dudash, M. R., Fenster, C. B., Lacy, R. C., & Sunnucks, P. (2019). A practical guide for genetic management of fragmented animal and plant populations. Oxford University Press.
- Frederico, R. G., De Marco, P., & Zuanon, J. (2014). Evaluating the use of macroscale variables as proxies for local aquatic variables and to model stream fish distributions. *Freshwater Biology*, 59(11), 2303–2314.
- Fu, X., Cohen, T. J., & Arnold, L. J. (2017). Extending the record of lacustrine phases beyond the last interglacial for Lake Eyre in Central Australia using luminescence dating. *Quaternary Science Reviews*, 162, 88–110.
- Fujioka, T., & Chappell, J. (2010). History of Australian aridity: Chronology in the evolution of arid landscapes. *Geological Society, London, Special Publications*, 346(1), 121–139.
- Garrick, R. C., Bonatelli, I. A. S., Hyseni, C., Morales, A., Pelletier, T. A., Perez, M. F., Rice, E., Satler, J. D., Symula, R. E., Thomé, M. T. C., & Carstens, B. C. (2015). The evolution of phylogeographic data sets. *Molecular Ecology*, 24(6), 1164–1171. https://doi.org/10.1111/ mec.13108
- Gavin, D. G., Fitzpatrick, M. C., Gugger, P. F., Heath, K. D., Rodríguez-Sánchez, F., Dobrowski, S. Z., Hampe, A., Hu, F. S., Ashcroft, M. B., Bartlein, P. J., Blois, J. L., Carstens, B. C., Davis, E. B., de Lafontaine, G., Edwards, M. E., Fernandez, M., Henne, P. D., Herring, E. M., Holden, Z. A., & Williams, J. W. (2014). Climate refugia: Joint inference from fossil records, species distribution models and phylogeography. *New Phytologist*, 204(1), 37–54. https://doi.org/10.1111/ nph.12929
- GonÇalves, D. V., Pereira, P., Velo-AntÓn, G., Harris, D. J., Carranza, S., & Brito, J. C. (2018). Assessing the role of aridity-induced vicariance and ecological divergence in species diversification in north-West Africa using agama lizards. *Biological Journal of the Linnean Society*, 124(3), 363–380.
- Hindar, K., Ryman, N., & Utter, F. (1991). Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 945–957.
- Hoang, D. T., Chernomor, O., von Haeseler, A., Minh, B. Q., & Vinh, L. S. (2017). UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35(2), 518–522.
- Hughes, J. M., Baker, A. M., Bartlett, C., Bunn, S., Goudkamp, K., & Somerville, J. (2004). Past and present patterns of connectivity among populations of four cryptic species of freshwater mussels *Velesunio* spp. (Hyriidae) in Central Australia. *Molecular Ecology*, 13(10), 3197-3212.
- Hughes, J. M., & Hillyer, M. J. (2003). Patterns of connectivity among populations of *Cherax destructor* (Decapoda: Parastacidae) in western Queensland, Australia. *Marine and Freshwater Research*, 54(5), 587-596.
- Hunt, T. L., & Jones, P. (2018). Informing the great fish stocking debate: An Australian case study. *Reviews in Fisheries Science and Aquaculture*, 26(3), 275–308.
- Jerry, D. (2008). Phylogeography of the freshwater catfish *Tandanus tandanus* (Plotosidae): A model species to understand evolution of

-WILE

WILEY- Journa Biogeo

the eastern Australian freshwater fish fauna. Marine and Freshwater Research, 59, 351–360.

- Jerry, D., Elphinstone, M. S., & Baverstock, P. R. (2001). Phylogenetic relationships of Australian members of the family Percichthyidae inferred from mitochondrial 12S rRNA sequence data. *Molecular Phylogenetics and Evolution*, 18(3), 335–347.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4(1), 170122. https://doi.org/10.1038/ sdata.2017.122
- Kautt, A. F., Machado-Schiaffino, G., & Meyer, A. (2016). Multispecies outcomes of sympatric speciation after admixture with the source population in two radiations of Nicaraguan crater lake cichlids. *PLoS Genetics*, 12(6), e1006157.
- Kearns, A. M., Joseph, L., Toon, A., & Cook, L. G. (2014). Australia's arid-adapted butcherbirds experienced range expansions during Pleistocene glacial maxima. *Nature Communications*, 5(1), 3994.
- Kidd, D. M., & Ritchie, M. G. (2006). Phylogeographic information systems: Putting the geography into phylogeography. *Journal of Biogeography*, 33(11), 1851–1865.
- Kireta, D., Christmas, M. J., Lowe, A. J., & Breed, M. F. (2019). Disentangling the evolutionary history of three related shrub species using genome-wide molecular markers. *Conservation Genetics*, 20(5), 1101–1112.
- Larkin, Z. T., Ralph, T. J., Tooth, S., Fryirs, K. A., & Carthey, A. J. R. (2020). Identifying threshold responses of Australian dryland rivers to future hydroclimatic change. *Scientific Reports*, 10(1), 6653.
- Leigh, C., Bush, A., Harrison, E. T., Ho, S. S., Luke, L., Rolls, R. J., & Ledger, M. E. (2015). Ecological effects of extreme climatic events on riverine ecosystems: Insights from Australia. *Freshwater Biology*, 60(12), 2620–2638.
- Lintermans, M. (2007). Fishes of the Murray-Darling basin: An introductory guide. Murray-Darling Basin Commission.
- Martin, H. A. (2006). Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of Arid Environments*, 66(3), 533–563.
- McCormack, J. E., Hird, S. M., Zellmer, A. J., Carstens, B. C., & Brumfield, R. T. (2013). Applications of next-generation sequencing to phylogeography and phylogenetics. *Molecular Phylogenetics and Evolution*, 66(2), 526–538.
- Meirmans, P. G. (2020). Genodive version 3.0: Easy-to-use software for the analysis of genetic data of diploids and polyploids. *Molecular Ecology Resources*, 20(4), 1126–1131.
- Minh, B. Q., Hahn, M. W., & Lanfear, R. (2020). New methods to calculate concordance factors for phylogenomic datasets. *Molecular Biology* and Evolution, 37(9), 2727–2733.
- Mossop, K. D., Adams, M., Unmack, P. J., Smith Date, K. L., Wong, B. B. M., & Chapple, D. G. (2015). Dispersal in the desert: Ephemeral water drives connectivity and phylogeography of an arid-adapted fish. *Journal of Biogeography*, 42(12), 2374–2388.
- Murphy, A. L., Pavlova, A., Thompson, R., Davis, J., & Sunnucks, P. (2015). Swimming through sand: Connectivity of aquatic fauna in deserts. *Ecology and Evolution*, 5(22), 5252–5264.
- Musyl, M. K., & Keenan, C. P. (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(6), 1585–1601.
- Nanson, G. C., Price, D. M., Jones, B. G., Maroulis, J. C., Coleman, M., Bowman, H., Cohen, T. J., Pietsch, T. J., & Larsen, J. R. (2008). Alluvial evidence for major climate and flow regime changes during the middle and late quaternary in eastern Central Australia. *Geomorphology*, 101(1), 109–129. https://doi.org/10.1016/j.geomo rph.2008.05.032

- Nguyen, L., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32(1), 268–274.
- Otto-Bliesner, B. L., Marshall, S. J., Overpeck, J. T., Miller, G. H., & Hu, A. (2006). Simulating Arctic climate warmth and icefield retreat in the last interglaciation. *Science*, 311(5768), 1751–1753.
- Pahad, G., Montgelard, C., & van Vuuren, B. J. (2020). Phylogeography and niche modelling: Reciprocal enlightenment. *Mammalia*, 84(1), 10–25. https://doi.org/10.1515/mammalia-2018-0191
- Paillard, D. (2006). What drives the ice age cycle? *Science*, 313(5786), 455-456.
- Park, C., Jeong, S., Joshi, M., Osborn, T. J., Ho, C., Piao, S., Chen, D., Liu, J., Yang, H., Park, H., Kim, B., & Feng, S. (2018). Keeping global warming within 1.5°C constrains emergence of aridification. Nature. *Climate Change*, 8(1), 70–74. https://doi.org/10.1038/ s41558-017-0034-4
- Pepper, M., Fujita, M., Moritz, C., & Keogh, J. (2011). Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone. *Molecular Ecology*, 20(7), 1529–1545.
- Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One*, 7(5), e37135.
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3), 231–259.
- Pickrell, J. K., & Pritchard, J. K. (2012). Inference of population splits and mixtures from genome-wide allele frequency data (inferring history from genetics). *PLoS Genetics*, 8(11), e1002967.
- Pusey, B., Kennard, M. J., & Arthington, A. H. (2004). Freshwater fishes of North-Eastern Australia. CSIRO publishing.
- Reynolds, L. F. (1983). Migration patterns of five fish species in the Murray-Darling river system. *Marine and Freshwater Research*, 34(6), 857–871.
- Richards, C. L., Carstens, B. C., & Knowles, L. L. (2007). Distribution modelling and statistical phylogeography: An integrative framework for generating and testing alternative biogeographical hypotheses. *Journal of Biogeography*, 34(11), 1833–1845.
- Rivers, D. M., Darwell, C. T., & Althoff, D. M. (2016). Phylogenetic analysis of RAD-seq data: Examining the influence of gene genealogy conflict on analysis of concatenated data. *Cladistics*, 32(6), 672–681.
- Rosenberg, N. A., & Nordborg, M. (2002). Genealogical trees, coalescent theory and the analysis of genetic polymorphisms. *Nature Reviews Genetics*, 3(5), 380–390.
- Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30(9), 1312–1313.
- Thacker, C. E., Unmack, P. J., Matsui, L., & Rifenbark, N. (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(9), 1518–1533.
- Unmack, P. J. (2001). Biogeography of Australian freshwater fishes. Journal of Biogeography, 28(9), 1053–1089.
- Unmack, P. J., Sandoval-Castillo, J., Hammer, M. P., Adams, M., Raadik, T. A., & Beheregaray, L. B. (2017). Genome-wide SNPs resolve a key conflict between sequence and allozyme data to confirm another threatened candidate species of river blackfishes (Teleostei: Percichthyidae: Gadopsis). *Molecular Phylogenetics and Evolution*, 109, 415–420.
- Unmack, P. J., Young, M. J., Gruber, B., White, D., Kilian, A., Zhang, X., & Georges, A. (2019). Phylogeography and species delimitation of *Cherax destructor* (Decapoda: Parastacidae) using genome-wide SNPs. *Marine and Freshwater Research*, 70(6), 857–869.



- Veevers, J. J. (1984). Phanerozoic earth history of Australia. Clarendon Press.
- Victorian Fisheries Authority. (2020). Native fish releases 2020. Retrieved from https://vfa.vic.gov.au/recreational-fishing/fish-stocking/fishstocking-reporting/native-fish-releases/nativefish2020
- Waters, J. M., Burridge, C. P., & Craw, D. (2019). The lasting biological signature of Pliocene tectonics: Reviewing the re-routing of Australia's largest river drainage system. Journal of Biogeography, 46(7), 1494-1503.
- Williams-Subiza, E. A., & Epele, L. B. (2021). Drivers of biodiversity loss in freshwater environments: A bibliometric analysis of the recent literature. Aquatic Conservation: Marine and Freshwater Ecosystems, 31(9), 1–12.

BIOSKETCH

The authors have broad interests on evolution, ecology and conservation management of aquatic organisms, particularly teleosts. For more information visit: www.molecularecology.flinders.edu. au/publications

Author Contributions: LBB designed and supervised the project; DMG, PU and LBB performed fieldwork; CRMA and JSC generated the data; EJB performed data analysis with assistance from JSC; EJB drafted the manuscript; co-authors revised the manuscript and approved its final version.

SUPPORTING INFORMATION

urnal of

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Booth, E. J., Sandoval-Castillo, J., Attard, C. R., Gilligan, D. M., Unmack, P. J. & Beheregaray, L. B. (2022). Aridification-driven evolution of a migratory fish revealed by niche modelling and coalescence simulations. Journal of Biogeography, 00, 1–13. https://doi.org/10.1111/ jbi.14337