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Ecological disturbance influences adaptive divergence despite high gene flow in golden perch (*Macquaria ambigua*): Implications for management and resilience to climate change

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Abstract

Populations that are adaptively divergent but maintain high gene flow may have greater resilience to environmental change as gene flow allows the spread of alleles that have already been tested elsewhere. In addition, populations naturally subjected to ecological disturbance may already hold resilience to future environmental change. Confirming this necessitates ecological genomic studies of high dispersal, generalist species. Here we perform one such study on golden perch (*Macquaria ambigua*) in the Murray-Darling Basin (MDB), Australia, using a genome-wide SNP data set. The MDB spans across arid to wet and temperate to subtropical environments, with low to high ecological disturbance in the form of low to high hydrological variability. We found high gene flow across the basin and three populations with low neutral differentiation. Genotype–environment association analyses detected adaptive divergence predominantly linked to an arid region with highly variable riverine flow, and candidate loci included functions related to fat storage, stress and molecular or tissue repair. The high connectivity of golden perch in the MDB will likely allow locally adaptive traits in its most arid and hydrologically variable environment to spread and be selected in localities that are predicted to become arid and hydrologically variable in future climates. High connectivity in golden perch is likely due to their generalist life history and efforts of fisheries management. Our study adds to growing evidence of adaptation in the face of gene flow and highlights the importance of considering ecological disturbance and adaptive divergence in biodiversity management.

KEYWORDS

ddRAD-seq, ecological genomics, environmental heterogeneity, generalist freshwater fish, landscape genomics, riverscape genomics

1 | INTRODUCTION

Geographic isolation and subsequent genetic drift, mutation and natural selection have historically been seen as the processes underpinning evolutionary biology (Futuyma & Mayer, 1980; Mayr, 1963). It is now widely recognized that natural selection can overcome

geographic and genetic connectivity when there is environmental heterogeneity, leading to adaptive divergence (Jones et al., 2012; Pavey et al., 2015; Sanford & Kelly, 2011) through various genomic mechanisms (Tigano & Friesen, 2016). Modelling and experiments have been used to examine this complex balance between gene flow, genetic drift and natural selection, and to predict the influence

of environmental heterogeneity and rapid environmental change (Lenormand, 2002; Bridle & Vines, 2007; Leimu & Fischer, 2008; Joe Hereford, 2009; Blanquart & Gandon, 2011; Blanquart, Gandon, & Nuismer, 2012; Blanquart & Gandon, 2014; Bourne et al., 2014; Polechová & Barton, 2015). The prevalence of adaptive divergence with gene flow in nature remains uncertain, but has been increasingly studied (Jones et al., 2012; Pavey et al., 2015; Sanford & Kelly, 2011) and is expected to be advantageous for populations facing future ecological disturbance.

Ecological disturbance is often defined as “any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment” (White & Pickett, 1985; also see Banks et al., 2013). It could be spurred by a wide range of events including natural fires, earthquakes or cyclones, human fragmentation and urbanization, as well as interannual or seasonal variance in rainfall or temperature. Ecological disturbance is known to influence patterns of neutral and adaptive genetic diversity in natural populations by impacting biological and demographic processes, spatial and temporal variation in habitat suitability, and natural selection and evolution (reviewed in Banks et al. (2013)). Populations that are often subjected to

ecological disturbance are thought to be more resilient to environmental change as they are already under selection for adaptive genetic variation that allows them to persist despite ecological disturbance (D’Odorico & Bhattachan, 2012; Tielbörger & Salguero-Gómez, 2014). High gene flow across environmentally heterogeneous environments, including ecologically stable to disturbed environments, could contribute to population persistence by inflating effective population size (N_e), allowing the maintenance of standing genetic variation that can promote rapid adaptive responses, and maximizing the spread of potentially adaptive alleles to newly altered habitats (Barrett & Schluter, 2008). In this way, a well-connected metapopulation spanning a wide range of environments may be inherently suited to adapt and persist in the face of heightening human-induced environmental change.

High environmental heterogeneity, including ecologically stable to disturbed environments, is typified in the Murray-Darling Basin (MDB), Australia. As one of Australia’s largest basins, it spans more than 1 million km² across a range of hydroclimatic environments from arid to wet, temperate to subtropical and unpredictable to stable riverine flow (Figure 1). Human-induced climate change is expected to increase flow variability and aridity in Australia

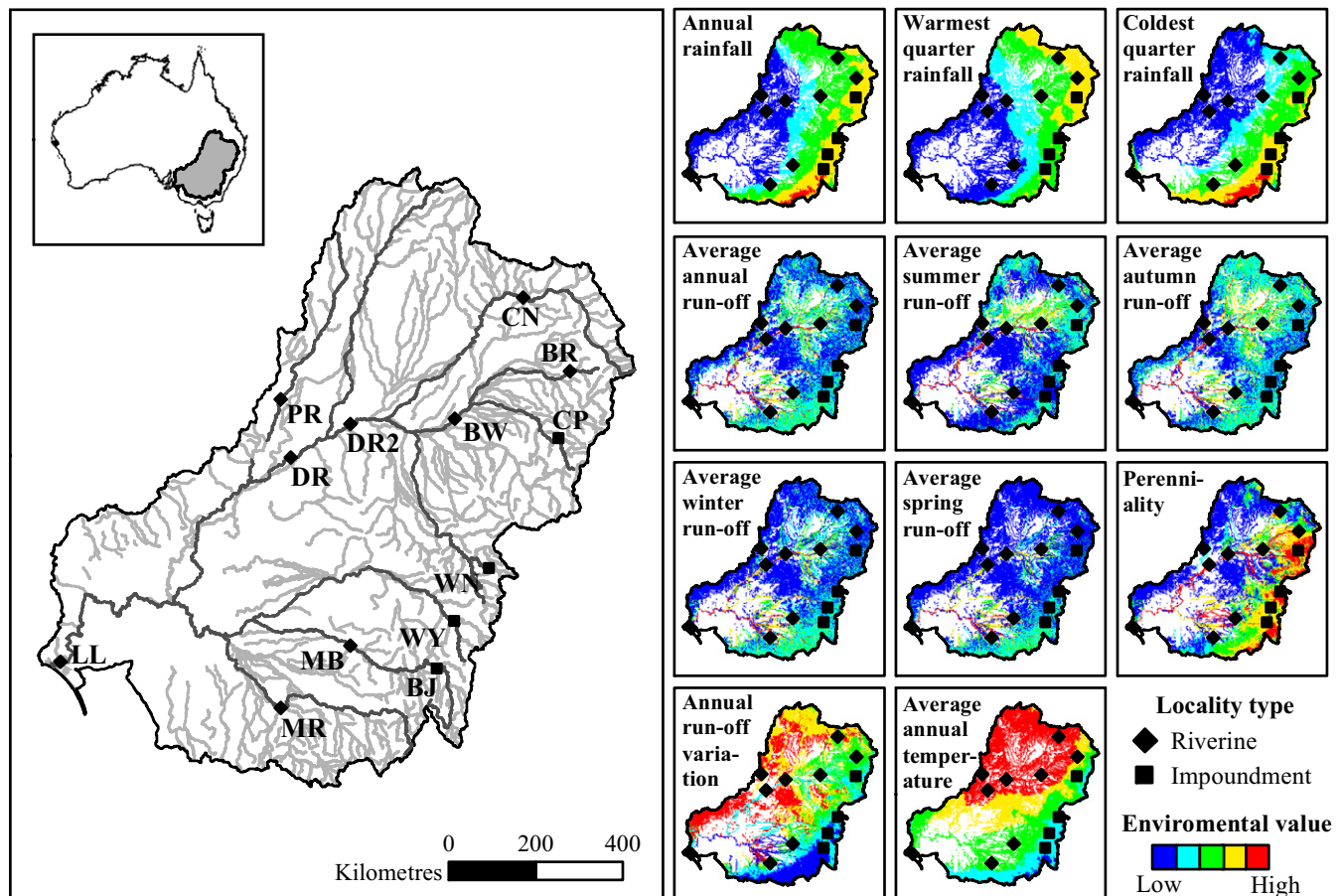


FIGURE 1 Map of the Murray-Darling Basin (MDB) in Australia, which shows the location of the MDB in Australia, the sampling localities for golden perch within the MDB, and the relative values across the basin of the eleven environmental variables used for the genotype—environment association analysis (see Table S2 for absolute values). The geometrical interval classification method was used in ARCGIS for colour-coding the environmental values. The localities are coded following Table 1

(Balcombe et al., 2011; Kingsford et al., 2011), making investigations of fishes across environmentally heterogeneous regions a first step in determining whether Australia's freshwater biotas may already hold the genetic variation required to cope with future climate change. The MDB has a high richness of freshwater fishes relative to elsewhere in Australia, and these have evolved different life history strategies to cope with the varied environments (Humphries, King, & Koehn, 1999). Australian fishes with low dispersal potential typically show greater population structure than high dispersal species and, due to human-mediated environmental change such as in-stream structures like weirs, also show population fragmentation, decreases in N_e and local extinctions (Attard, Brauer, et al., 2016; Brauer, Hammer, & Beheregaray, 2016; Brauer, Unmack, Hammer, Adams, & Beheregaray, 2013; Cole et al., 2016; Coleman et al., 2010; Cook, Bunn, & Hughes, 2007; Cook, Kennard, Real, Pusey, & Hughes, 2011; Hammer, Adams, Unmack, & Walker, 2007; Hughes, Ponniah, Hurwood, Chenoweth, & Arthington, 1999; Hughes, Real, Marshall, & Schmidt, 2012; Lean, Hammer, Unmack, Adams, & Beheregaray, 2017; Sasaki, Hammer, Unmack, Adams, & Beheregaray, 2016; Woods, Macdonald, Crook, Schmidt, & Hughes, 2010). A genome-wide population study of a low dispersal, habitat specialist fish in the MDB, the southern pygmy perch (*Nannoperca australis*), showed low levels of standing genetic variation in remaining population fragments and adaptive divergence related to temperature, rainfall and riverine flow heterogeneity (Brauer et al., 2016). On the other hand, the only other genome-wide study of a MDB fish was of Murray cod (*Maccullochella peelii*), a moderate disperser that showed low to moderate population structure and, despite relatively high gene flow, adaptive divergence related to temperature and rainfall (the potential influence of flow was not assessed) (Harrison et al., in press). Australian fishes with high dispersal potential and larger N_e are expected to maintain higher levels of standing genetic variation, especially if they are also ecological generalists, and may already occupy areas of high ecological disturbance, making them perhaps able to withstand future increases in flow variability and aridity.

One such species in the MDB is the golden perch (*Macquaria ambigua*): a medium-large sized, long-lived freshwater fish (length = 35–50 cm; sexual maturity = 2 years males, 4 years females; longevity = 26 years; Mallen-Cooper and Stuart (2003)). Golden perch in the MDB have a high genetic diversity relative to golden perch in other basins (Faulks, Gilligan, & Beheregaray, 2010b), which are thought to represent different, but closely related and currently undescribed species (Beheregaray et al., 2017; Faulks, Gilligan, & Beheregaray, 2010a). The high diversity of MDB golden perch has been attributed to their high genetic connectivity and relatively large N_e , likely driven by high spring-time flow in the MDB (Faulks et al., 2010b). Golden perch have long been known to respond to environmental change: they take advantage of warm water temperatures and high-flow flood events in spring and summer by migrating hundreds or even thousands of kilometres upstream to presumably spawn, with their buoyant eggs and larvae subsequently drifting downstream (Lake, 1967; Mackay, 1973;

Reynolds, 1976, 1983). The homogenizing influence of their long-range movements on neutral genetic structure has previously been shown using microsatellites and allozymes (Faulks et al., 2010b; Musyl & Keenan, 1992). Their movements and reproductive response to environmental cues have, however, been revealed recently as more complex: they can disperse downstream for spawning (Koster et al., 2017), in-channel, nonflood flow can trigger smaller episodes of upstream migration and spawning (Mallen-Cooper & Stuart, 2003; Zampatti & Leigh, 2013a,b), and they can spawn in relatively cold, nonflood conditions in arid areas (Balcombe et al., 2006; Ebner, Scholz, & Gawne, 2009; Kerezszy, Balcombe, Arthington, & Bunn, 2011). This is potentially due to the evolution of life history strategies for different environmental conditions in the MDB, such as spawning in the arid environment during suboptimal flow conditions because of the unpredictability of rainfall. This, along with their preference for warm environments, is thought to give the species an advantage relative to many other freshwater fishes in Australia's predicted future climates of aridity and flow instability (Balcombe et al., 2011).

Understanding adaptive (i.e., ecologically relevant) variation potentially allows the incorporation of such information into conservation and management practices (Funk, McKay, Hohenlohe, & Allendorf, 2012; Hoffmann et al., 2015; but see Shaffer et al., 2015; Garner et al., 2016; Pearse, 2016; Allendorf, 2017). For instance, this could be used to define adaptive-based management units that, in high gene flow species, may be subsets within classic neutral-based units (Funk et al., 2012). Consideration of adaptive variation in management is already of relevance to golden perch. The species is recreationally fished throughout the MDB and commercially fished in the lower reaches of the MDB. As a management response, the number of golden perch at some river system localities and hydrologically isolated impoundments are augmented by stocking from hatcheries (Ferguson & Ye, 2012). Stocked fish in the river system can outnumber wild-born golden perch at release sites and disperse to influence the demographics and, potentially, the genetic composition of surrounding localities (Crook et al., 2016; Forbes et al., 2016). To minimize the impact of stocking on the genetic diversity of the natural system, hatcheries are only allowed to source broodstock and then release their progeny at a regional level in the MDB (NSW Department of Primary Industries 2010; Rowland, 1996; Rowland & Tully, 2004). Microsatellite analyses of stocked impoundments in the MDB show they have little or no neutral genetic differentiation to localities in the natural river system (Faulks et al., 2010b), as one would expect if broodfish are correctly being sourced. Management practices may also benefit from determining if impoundments include highly related individuals as this is a common issue in aquaculture (Brown, Woolliams, & McAndrew, 2005; Liu et al., 2012; Loughnan et al., 2013).

Here, we use a genome-wide SNP data set to test the hypothesis that marked environmental heterogeneity, and in particular varying levels of ecological disturbance, can overwhelm the homogenizing effect of gene flow and lead to adaptive divergence. We use a ddRAD data set of golden perch from across its range in

the highly heterogeneous environment of the MDB. Environmental attributes examined in our genotype–environment association analysis encompass flow, temperature and rainfall due to their known ecological relevance to freshwater fishes (e.g., Brauer et al., 2016; Faulks et al., 2010b; Harrison et al., in press) and expected future increases in temperature and flow variability. To examine the selective influence of ecological disturbance, we focus on whether average flow, variance in flow or both affect adaptive divergence. This is of import to the ecosystem as a whole as hydrologic regime is a main driver of ecosystem structure and function (Poff et al., 1997) and natural hydrologic variance may increase an ecosystem's resilience to future environmental change (D'Odorico & Bhattachan, 2012). Given the increased power of our genomic data set compared to previous data sets (Faulks et al., 2010a,b), we also re-examined neutral genetic structure of golden perch in the river system and impoundments, including novel estimation and assessment of relatedness. We anticipate that this study will impact the management of golden perch stocks and water resources across the MDB—the most important agricultural region in Australia and one of the world's most degraded freshwater systems (CSIRO 2008; Palmer et al., 2008). More broadly, our study provides one of the first applications of landscape genomics to clarify our empirical-based understanding of evolution through adaptation in the presence of gene flow and of adaptation to ecologically disturbed environments.

2 | METHODS

2.1 | Population genomic data collection

Tissue was collected from 173 fish in 13 localities across the geographic and environmental range of the species in the MDB (Figure 1). The tissue was either from fin clips of anaesthetized fish that were then immediately released to the capture locality or from fin clips or muscle of euthanized fish (see Acknowledgements for research permit and ethics clearance). The sampling design was informed by previous studies in the MDB that clarified the neutral metapopulation structure of golden perch using 590 individuals from 26 localities (Faulks et al., 2010a,b) and the environmental variables of interest for adaptation across the basin for a native fish (Brauer et al., 2016).

Our samples include previously used samples from across the species' range in the MDB (Faulks et al., 2010a,b) plus the Lower Lakes—this represents the terminal region of the Murray River in the MDB, a key sample not included in Faulks et al. (2010a,b). All localities are in separate rivers, except for two localities from the Darling River. The sampling dates across localities range from 2004 to 2015 (Table 1), which makes it possible for detected adaptive divergences between localities to be driven by temporal differences in sample collection. However, this is unlikely as genotype–environment associations were conducted based on environmental data aggregated across three decades (see Environmental data collection) rather than data collected at the time of sampling. This allowed us to ascertain relatively long-term environmental attributes of MDB

TABLE 1 Genetic variation of golden perch in the MDB and additional information for each sampling locality at the 3,139 SNPs. *n*, sample size (after filtering individuals based on missing data and replicate samples); AR, allelic richness; *H_o*, mean observed heterozygosity; *H_e*, mean unbiased expected heterozygosity; *F_{IS}*, inbreeding coefficient. In parentheses are the standard deviations

Locality code	River	Impoundment name	Sampling date (MM/YYYY)	<i>n</i>	% missing data	AR	% polymorphic loci	<i>H_o</i>	<i>H_e</i>	<i>F_{IS}</i>
PR	Paroo	—	09/2013	14	11	1.70	79	0.222 (0.212)	0.244 (0.187)	0.058 (0.356)
DR	Darling	—	11/2002–02/2005	11	14	1.76	80	0.280 (0.248)	0.256 (0.188)	−0.117 (0.314)
DR2	Darling	—	05/2014	15	10	1.77	87	0.219 (0.194)	0.266 (0.176)	0.138 (0.372)
CN	Condamine	—	05/2006	14	2	1.77	90	0.294 (0.227)	0.275 (0.173)	−0.082 (0.289)
BW	Barwon	—	02/2005	11	5	1.77	86	0.297 (0.241)	0.271 (0.181)	−0.118 (0.299)
BR	Borders	—	04/2005	13	6	1.79	90	0.324 (0.245)	0.281 (0.174)	−0.153 (0.277)
MB	Murrumbidgee	—	09/2004	9	3	1.77	84	0.310 (0.252)	0.275 (0.183)	−0.156 (0.304)
MR	Murray	—	09/2004–03/2005	9	13	1.76	76	0.267 (0.251)	0.251 (0.193)	−0.106 (0.347)
LL	Lower Lakes	—	04/2015	11	3	1.76	85	0.301 (0.244)	0.271 (0.183)	−0.128 (0.290)
CP	Gwydir	Copeton	—/2006	12	6	1.76	85	0.294 (0.239)	0.270 (0.181)	−0.107 (0.304)
WN	Macquarie	Windamere	—/2006	14	4	1.77	88	0.326 (0.251)	0.280 (0.178)	−0.159 (0.283)
WY	Lachlan	Wyangala	05/2006	10	8	1.76	81	0.301 (0.254)	0.267 (0.187)	−0.152 (0.307)
BJ	Murrumbidgee	Burrinjuck	09/2006	16	3	1.76	90	0.321 (0.249)	0.274 (0.176)	−0.157 (0.272)

been used by our research group to successfully assess adaptation in a native fish across the MDB (Brauer et al., 2016).

2.3 | Genetic variation and structure

The genomic DNA was checked for quality using a spectrophotometer (NanoDrop, Thermo Scientific), integrity using 2% agarose gels and quantity using a fluorometer (Qubit, Life Technologies). Libraries were prepared following the ddRAD protocol of Peterson, Weber, Kay, Fisher, and Hoekstra (2012) with modifications as described in Brauer et al. (2016) (except using 300–800 bp size selection here) and with restriction enzymes *Sbf*I and *Mse*I. Each set of 48 samples was paired-end 100 bp sequenced (Illumina HiSeq 2000) on a separate lane at the McGill University and Génome Québec Innovation Centre, Canada. Resulting reads were processed using the de novo pipeline of STACKS 1.29 (Catchen, Hohenlohe, Basham, Amores, & Cresko, 2011; Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2013) to produce a final SNP data set (Supporting Information).

2.2 | Environmental data collection

We estimated pairwise relatedness between individuals using COANCESTRY 1.0.1.6 (Wang, 2011) to assess the level of relatedness in fish from impoundments compared with those in the open river system and to ensure any detected high levels of relatedness could be taken into account when interpreting our population structure results. Pairwise relatedness was estimated based on the combined allele frequency of the whole data set and for each locality separately. We used all seven pairwise relatedness estimators available in COANCESTRY: the moment estimators of Queller and Goodnight (1989), Li, Weeks, and Chakravarti (1993), Ritland (1996), Lynch and Ritland (1999) and Wang (2002), and the dyadic maximum-likelihood estimator of Milligan (2003) and triadic maximum-likelihood estimator of Wang (2007) (100 reference individuals for the triadic estimator).

Consistency in trends across estimators would mean the trends are robust to the estimator being used even though the accuracy and precision of different estimators can depend on the data set (van de Castele, Galbusera, & Matthysen, 2001).

2.4 | Identifying signatures of selection and spatial adaptive divergence

Markers potentially under directional selection were identified from the SNP data set using methods based on F_{ST} outlier tests and genotype–environment association. This was performed after excluding impoundments from the data set given the genetic make-up of impoundments would be dictated largely by the environment in hatcheries, especially because of the lack of local recruitment in impoundments and their hydrological isolation (Forbes et al., 2016), and assessing selection due to captivity is beyond the scope of this study. Given the relatively high environmental distinctness of the arid-zone Paroo River (see Results), the analyses were also performed with and without Paroo River to assess the degree that this location was driving signals of selection.

The F_{ST} outlier tests used were the Bayesian method of BAYESCAN 2.1 (Foll & Gaggiotti, 2008) and the coalescent-based method of $FDIS_{\tau 2}$ (Beaumont & Nichols, 1996) as implemented in LOSITAN (Antao, Lopes, Lopes, Beja-Pereira, & Luikart, 2008) (default number of simulations [50,000] with addition of “neutral” and “force” mean F_{ST} options). We used a false discovery rate (FDR) of 0.1 to correct for type I errors from multiple testing. Both these programs simultaneously detect loci under either balancing or directional selection. However, loci under balancing selection are expected to have lower differentiation than neutral loci (and loci under directional selection have greater differentiation), making it problematic to discern balancing selection in biological systems with low or no neutral structure (Beaumont & Balding, 2004). So, we only extracted loci from these programs that showed evidence for directional selection.

The genotype–environment association analysis was implemented in GINLAND (Guillot, Vitalis, Al, & Gautier, 2014), which compares a model where the environmental variable of interest has an influence on the allele frequencies of the locus in question with a model where that variable has no influence. This method also takes into account the potential influence of spatial structure using the x and y coordinates of localities. We generated x and y coordinates by calculating pairwise river distances between localities using ARCGIS 10.2 (ESRI) and performing multidimensional scaling (MDS) using the *cmdscale* base function of R (R Core Team 2015) to convert these river distances to representative coordinates. We did not use the geographic x and y coordinates as they are inappropriate in river-scape studies due to the dendritic spatial structure of river systems. The representative coordinates were used to estimate the spatial covariance structure of the allele frequency data for a random subset of 500 loci (due to computational time) using all individuals, as recommended by Guillot et al. (2014). GINLAND was then run for each environmental variable, with the estimated spatial covariance parameters controlling for spatial structure, and loci were extracted

for subsequent analysis if they had a log Bayes factor greater than three following Jeffreys (1961) and Kass and Raftery (1995). As GINLAND is a univariate model, just one environmental variable is tested per run. Thus, even if there is covariation among some variables, all environmental variables can be retained for these analyses.

Candidate loci were conservatively chosen as those identified in at least one outlier and one genotype–environment association, either when using the complete data set or using the data set without the Paroo River. These loci were further examined for functional annotation by running a BLAST search (Camacho et al., 2009) using a forward and reverse read from a representative individual with the least amount of missing data (in the unlikely event that a locus was not present in this individual, it would be extracted from the next individual with the least amount of missing data). The BLAST search was performed in BLAST2GO (Conesa et al., 2005) using the NCBI full database (BLASTN) and nonredundant nucleotide database (BLASTX). We only considered hits from characterized loci that were above an e -value threshold of 1×10^{-5} and, in cases of multiple hits for a single locus, we retained only the hit with the greatest e -value.

3 | RESULTS

3.1 | Data collection

A range from 168,685,784 to 191,669,589 forward reads per lane with an average of 182,396,612 per lane and a total of 911,983,062 across lanes were generated using the Illumina platform. After demultiplexing, a range from 261,324 to 4,189,190 reads, with an average of 1,568,183 reads, were obtained per individual, totalling 291,682,051 reads. De novo assembly and catalogue filtering to generate a SNP data set revealed that 13 individuals spread across 10 sampling localities had a high (>30%) amount of missing data. They were therefore removed and the catalogue refiltered. This resulted in 3,636 SNPs, with a final data set of 3,139 SNPs (total 7% missing data; see Table 1 for missing data per locality) obtained by extracting only the first SNP from each ddRAD locus.

3.2 | Environmental variation

The eleven environmental variables showed high heterogeneity across the MDB. The general environmental trends (Figure 1) include an east–west gradient in annual rainfall, higher summer rainfall in the north-east and higher winter rainfall in the south-east. There is higher run-off (i.e., riverine flow) in the main rivers compared to the tributaries, with the exception of the arid zone towards central Australia which showed relatively low flows even in the main river (Paroo River). Perenniality tended to be greater in the eastern headwaters and the main rivers, and variation in annual run-off tended to be lowest in the south-east and the main rivers. Rainfall, run-off and perenniality are therefore not tightly correlated (Table S3). This is because in this system rainfall is positively associated with flow in the headwaters but is not associated with flow in the main rivers, where flows tend to be less variable

and can be derived from rainfall thousands of kilometres away. Different measures of average run-off—that is, average annual, summer, autumn, winter and spring run-off—showed correlations (Table S3), but still with differences in run-off between seasons due to higher summer rainfall (and associated run-off) in the north-east headwaters and higher winter rainfall (and associated run-off) in the south-east headwaters. Temperatures increased towards the arid region of the north-west (i.e., Paroo River), which also showed high variation in annual run-off and low perenniality, as expected for arid environments.

3.3 | High neutral connectivity across the basin

The sampling localities had similar levels of genome-wide variation (Table 1). Within localities, 76 to 90% of the SNPs were polymorphic, average observed heterozygosity (H_O) ranged from 0.222 to 0.326, average expected heterozygosity (H_E) ranged from 0.244 to 0.281, allelic richness ranged from 1.70 to 1.77 and F_{IS} ranged from -0.159 to 0.138 . An analysis of F_{IS} values over loci showed that values match that of a normal distribution with mean F_{IS} of -0.089 (Figure S2).

There was low to nil population structure and high connectivity across the basin, even among localities separated by almost 2,500 km and between the natural rivers and impoundments (Table 2, Figures 2 and 3). The most genetically differentiated locality in the river system, as shown in all analyses, was the Paroo River—which still showed high connectivity, with a maximum pairwise F_{ST} of 0.024. The Lower Lakes also included individuals that were genetically distinct according to F_{ST} analyses of all individuals from that locality, but there was also a subset of individuals from the Lower Lakes that were assigned by STRUCTURE to the greater MDB population. The impoundments, especially Burrinjuck Dam, showed evidence of containing closely related individuals but in all other respects were genetically similar to the fish in the river system.

Specifically, the PCA (Figure 2) clustered separately the Paroo River, a subset of individuals from the Lower Lakes, and some of the individuals in impoundments, especially Burrinjuck Dam. STRUCTURE (Figure 3) clustered all individuals from the Paroo River and, only when impoundments were removed, also clustered separately the subset of individuals from the Lower Lakes. When included, some individuals from impoundments grouped into distinct clusters. The likelihood across different values of K was similar up to a K of five and, when impoundments were excluded, a K of three, after which the likelihood became more variable across replicate runs and tended to decrease (Figure S3). This trend in likelihood values is different to that designed for use with the ΔK method of inferring K (Evanno et al., 2005), making the ΔK inference unreliable. There was low but significant evidence of genetic differentiation based on F_{ST} for pairwise comparisons, mostly between the Paroo River, Burrinjuck Dam and the Lower Lakes with each other and every other locality (Table 2). The relatedness estimates indicated that fish in impoundments had greater levels of relatedness compared to riverine localities, regardless of whether relatedness was estimated based on the

TABLE 2 Genetic differentiation (F_{ST}) of golden perch in the MDB. F_{ST} values > 0 are shaded grey. p values from permutation tests are in parentheses, with pairwise comparisons showing significant differentiation after sequential Bonferroni correction in bold and after no correction ($p < .05$) in italics

	PR	DR	DR2	CN	BW	BR	MB	MR	LL	CP	WN	WY	BJ
PR													
DR	-0.016 (1.000)												
DR2	0.018 (0.000)	-0.047 (1.000)											
CN	0.013 (0.000)	-0.043 (1.000)	-0.015 (1.000)										
BW	0.015 (0.000)	-0.038 (1.000)	-0.014 (1.000)	-0.005 (0.505)									
BR	0.009 (0.000)	-0.038 (1.000)	-0.020 (1.000)	-0.010 (0.998)	-0.009 (0.736)								
MB	0.015 (0.000)	-0.040 (1.000)	-0.012 (1.000)	-0.003 (0.998)	-0.006 (0.143)	-0.009 (0.333)							
MR	-0.029 (1.000)	-0.047 (1.000)	-0.057 (1.000)	-0.051 (1.000)	-0.046 (1.000)	-0.049 (1.000)	-0.054 (1.000)						
LL	0.024 (0.000)	-0.030 (1.000)	-0.002 (0.848)	0.007 (0.000)	0.005 (0.002)	0.001 (0.004)	0.005 (0.002)	-0.047 (1.000)					
CP	0.016 (0.000)	-0.033 (1.000)	-0.012 (1.000)	-0.004 (0.432)	-0.003 (0.135)	-0.015 (0.998)	-0.007 (0.361)	-0.040 (1.000)	0.006 (0.002)				
WN	0.023 (0.000)	-0.029 (1.000)	-0.005 (0.884)	0.005 (0.003)	0.002 (0.026)	-0.005 (0.173)	0.001 (0.041)	-0.036 (1.000)	0.014 (0.000)	0.000 (0.068)			
WY	0.008 (0.002)	-0.025 (0.999)	-0.019 (1.000)	-0.013 (0.990)	-0.012 (0.773)	-0.015 (0.936)	-0.019 (0.966)	-0.031 (1.000)	-0.006 (0.281)	-0.015 (0.892)	-0.006 (0.235)		
BJ	0.026 (0.000)	-0.024 (1.000)	0.002 (0.097)	0.010 (0.004)	0.012 (0.002)	0.005 (0.013)	0.006 (0.021)	-0.036 (1.000)	0.017 (0.001)	0.004 (0.027)	0.013 (0.001)	-0.012 (0.683)	

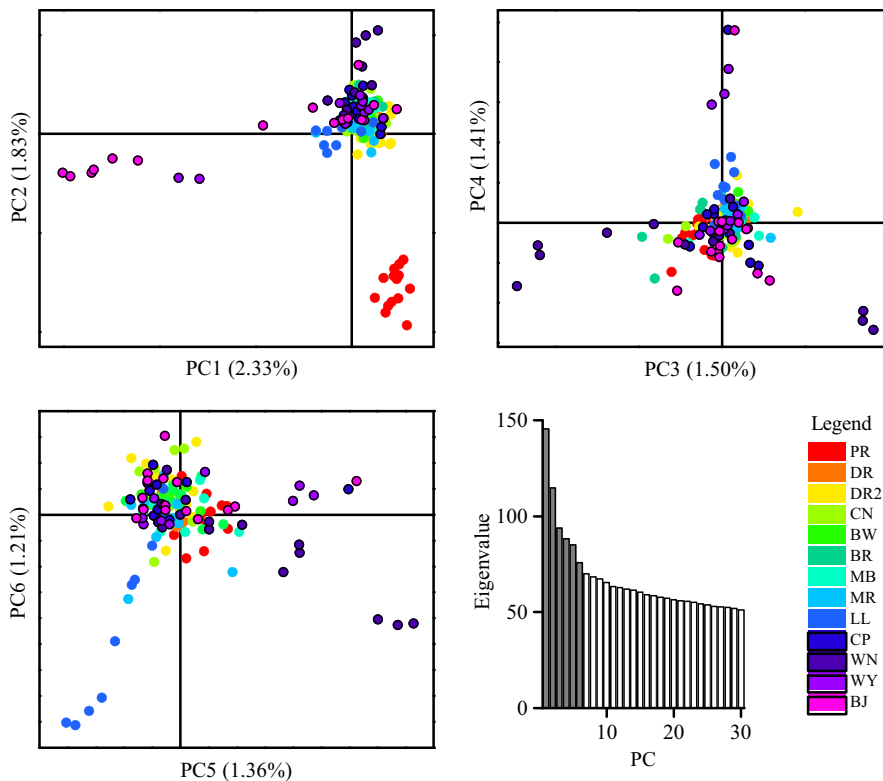


FIGURE 2 PCA of golden perch in the Murray-Darling Basin using 3,139 SNPs. PCs one to six, including the per cent of variance they each explain, and the eigenvalues of the first 30 PCs are shown. Individuals are represented as circles colour-coded according to their sampling locality, with circles representing samples from impoundments also having a black outline. Localities in the legend are coded following Table 1

allele frequency of the entire data set or each locality separately and regardless of the estimator used (Figure S4). This was corroborated by the PCA and STRUCTURE findings that showed genetic clustering of some related individuals in impoundments, especially in Burrinjuck Dam, and the F_{ST} findings of genetic differentiation of Burrinjuck Dam from other localities.

3.4 | Signatures of selection

The F_{ST} outlier methods of *FDIST2* and *BAYESCAN* identified 72 and 8 SNPs, respectively, and when not including the Paroo River in the data set, 43 and 4 SNPs, respectively. All SNPs detected using *BAYESCAN* were found by *FDIST2*. The difference in the number of loci between the F_{ST} outlier methods may be associated with *BAYESCAN* being more stringent than *FDIST2* (Narum & Hess, 2011). Unlike the F_{ST} outlier methods, the genotype–environment association method utilized environmental data. The genotype–environment association analysis identified 46 loci or 20 loci when not including the Paroo River in the data set. These were associated with one or a combination of six environmental attributes: average annual rainfall (number of associated SNPs: 2 or none without Paroo), average coldest quarter rainfall (16 or 6 without Paroo), average warmest quarter rainfall (3 or 5 without Paroo), variation in annual run-off (20 or 6 without Paroo), perenniality (13 or 9 without Paroo) and average annual temperature (21 or 10 without Paroo). None were associated with average run-off across the year or average run-off for each season. Using our conservative selection criteria for candidate loci—that they must be detected in at least one F_{ST} outlier and one genotype–environment test (see Methods)

—we selected 27 candidate loci when the Paroo River is included and 10 loci when excluding Paroo, with an overlap of six loci across the data sets (Figure 4). Combined across data sets, this results in a total of 31 candidate adaptive loci (Figures 4 and 5). These 31 SNPs represented one or a combination of all six previously identified environmental attributes: average annual rainfall (2 or none without Paroo), average coldest quarter rainfall (13 or 3 without Paroo), average warmest quarter rainfall (2 or 4 without Paroo), variation in annual run-off (14 or 3 without Paroo), perenniality (12 or 6 without Paroo) and average annual temperature (13 or 6 without Paroo). Twelve of the candidate loci were successfully annotated, with functions related to metabolism, including fat storage, as well as molecular and tissue repair, cell structure and signalling, and other functions (Figure 5).

4 | DISCUSSION

Golden perch were found to be a well-connected metapopulation in the MDB with low to nil basin-wide population structure. We also found that stocked fish in isolated impoundments are genetically similar to those in the open river system, but have unusually high relatedness, presumably as a consequence of hatchery breeding. The environmental analyses, however, disclosed marked environmental heterogeneity across the region. We hypothesized that environmental heterogeneity, especially varying levels of ecological disturbance, can overwhelm the homogenizing effect of gene flow and lead to adaptive divergence. Accordingly, integrative analyses of the genome-wide data set combined with environmental data found

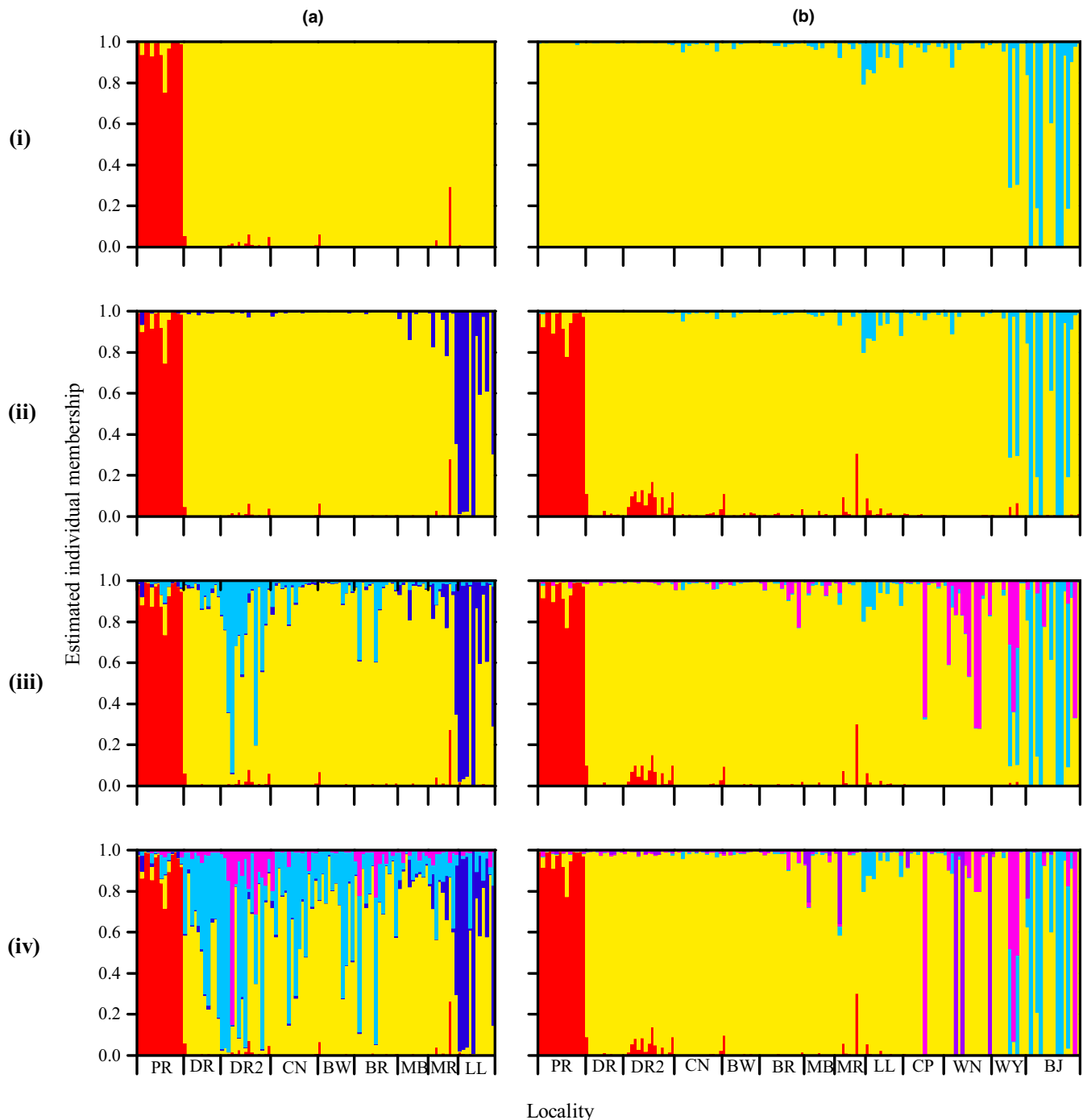


FIGURE 3 Clustering results of *STRUCTURE* analysis for golden perch in the Murray-Darling Basin using 3,139 SNPs. Shown are the clusters summarized using *CLUMPAK* for when *K* is set to (i) 2, (ii) 3, (iii) 4 and (iv) 5. The analysis was performed (a) without and (b) with impoundments included in the data set (impoundments are the last four localities). Clusters are colour-coded to represent their predominate locality: red, Paroo River; dark blue, Lower Lakes; yellow, other riverine localities; light blue, pink or purple, other clusters. Locality names are coded following Table 1

evidence of such adaptive divergence. Most of the candidate adaptive loci were associated with the Paroo River, the most arid and hydrologically disturbed drainage in the system. Associations were predominately due to variation in flow—rather than average flow—and also average annual temperature. This attests to the potential for ecological disturbance to maintain putatively adaptive variation

that can spread and thereby allow the persistence of golden perch, as well as other species (D'Odorico & Bhattachan, 2012; Tielbörger & Salguero-Gómez, 2014), in expected high disturbance regimes of the future (Balcombe et al., 2011). It also points to strong selection in relatively extreme environments of a species' range, such as arid and hydrologically variable environments in this case, and the

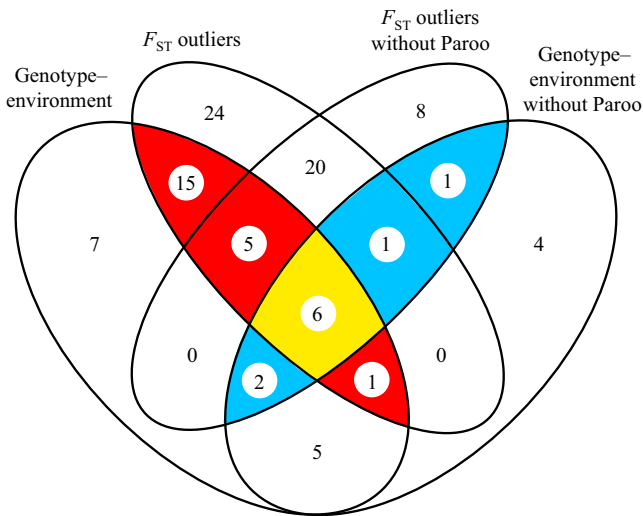


FIGURE 4 Venn diagram of loci putatively detected as being under adaptive divergence. Coloured sections are the loci conservatively chosen for further investigation (see Figure 5 legend) based on being detected by both a F_{ST} outlier and a genotype–environment association test, either with or without Paroo included in the data set

potential importance of these marginal environments to resilience in future climate scenarios (Hardie & Hutchings, 2010; Ledoux et al., 2015). This is opposed to what is expected in low dispersal, specialist species which typically have lower standing genetic variation and limited ability to spread adaptively beneficial variation to newly altered environments. Our results are therefore consistent with a scenario of adaptive divergence in the face of gene flow (Jones et al., 2012; Pavey et al., 2015; Sanford & Kelly, 2011) and showcase the influence of ecological disturbance in shaping intraspecific biodiversity, a topic of increasing importance given that disturbance regimes are changing rapidly in our human-modified world (Banks et al., 2013).

4.1 | A highly connected riverscape

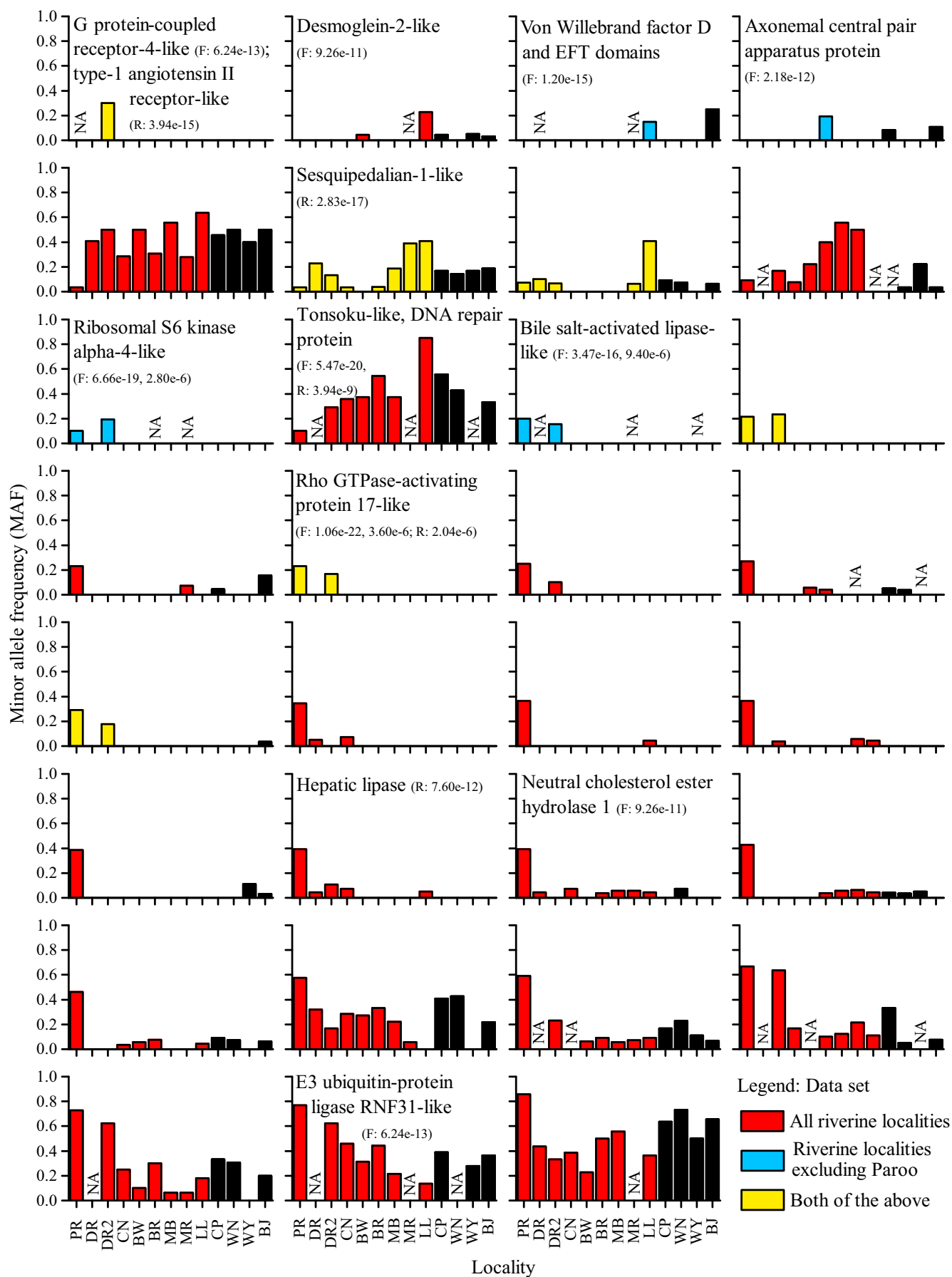
There was no evidence of neutral divergence across most of the Murray–Darling river system. The most genetically differentiated locality (excluding impoundments) was the Paroo River, as also found previously using microsatellites (Faulks et al., 2010b), but it still had a low F_{ST} of, at most, only 0.024 to other river localities. The Paroo is the most north-western drainage within the MDB and is generally an endorheic system ending in a terminal wetland, but its high

connectivity is maintained by large rainfall events that fill the floodplains to the south and hydrologically connect it to the Darling River approximately once every 25 years. The long lifespan of golden perch—26 years (Mallen-Cooper & Stuart, 2003)—means there would likely be an opportunity for riverine flow to facilitate their dispersal elsewhere in their lifetime. The only other river locality showing increased genetic distinctness was the Lower Lakes: there was low but significant genetic differentiation of the Lower Lakes to multiple localities. Interestingly, approximately half of the Lower Lakes individuals had high or admixed ancestry to the larger MDB river metapopulation (excluding Paroo). This pattern may be driven by a degree of in situ spawning in the Lower Lakes (Ferguson & Ye, 2016), with connectivity to the metapopulation maintained by upstream migration and spawning with fish from other localities, subsequent downstream drifting of larvae and eggs, and the active movements of adults from elsewhere to the Lower Lakes (Reynolds, 1983; Ye et al., 2015; Zampatti et al., 2015). Some individuals from the Murray River and its only sampled tributary, the Murrumbidgee River, showed genetic ancestry to the Lower Lakes, indicating connectivity is bidirectional. Emigration from the Lower Lakes did not appear to extend as far north as the Darling River and its tributaries.

It is likely that the degree of demographic connectivity in golden perch is temporally dynamic, as previously suggested (Faulks et al., 2010b). Age distribution data and strontium isotope signatures indicate that golden perch individuals in one region can disperse actively or, in their larval stage, passively across hundreds of kilometres depending on environmental conditions (Ferguson & Ye, 2016; Zampatti et al., 2015). For example, high river flow conditions in the Darling River triggered spawning of the fish in early 2010, and these progeny subsequently dispersed into the southern MDB when there was increased flow in those areas in late 2010 and early 2011 (Zampatti et al., 2015). There is evidence of continued movement thereafter of adults from upstream regions to the Lower Lakes (Ferguson & Ye, 2016). This is concordant with our genetic results, which show high connectivity between the Murray and the Darling river systems, and movement from upstream regions to the Lower Lakes.

The high genetic connectivity and wide distribution of golden perch in the MDB matches the pattern expected for a generalist fish with its high movement capabilities (Hughes, Schmidt, & Finn, 2009; Lucas & Baras, 2001). Another moderate disperser, Murray cod, also has high levels of genetic connectivity across the MDB (Harrison et al., in press; Rourke, McPartlan, Ingram, & Taylor, 2010, 2011). Conversely, dispersive species can have high genetic structure if they are ecological specialists, such as Macquarie perch (*Macquaria australasica*) in the MDB (Faulks, Gilligan, & Beheregaray, 2011).

FIGURE 5 Allele frequencies at the 31 candidate adaptive loci in golden perch from across the MDB. Localities in the legend are coded following Table 1, and columns of each graph are coloured according to whether the locus was identified if the arid-zone sample from Paroo River was excluded from the data set. Columns representing impoundments are coloured black and were not used for detecting candidate adaptive loci. The allele represented is the minor allele based on the combined allele frequency of the riverine localities, and loci are in ascending order of this allele's frequency in Paroo River. NA indicates missing data for the associated locality. The annotation, whether it was on the forward (F) or reverse sequence (R) or a combination, and the associated e-value are shown in brackets. If there is one e-value, it is from BLASTN search, and if there are two e-values, the second is from the BLASTX search



Fishes that are both ecological specialists and have low dispersal capabilities often have high genetic structure or narrow distributions (e.g., Brauer et al., 2013; Cole et al., 2016; Sasaki et al., 2016). In addition, the hierarchical, dendritic characteristics of the river system (Radinger & Wolter, 2015; Thomaz, Christie, & Knowles, 2016) and in-stream structures (such as dams) that can inhibit dispersal (Cole et al., 2016) further promote genetic structure in these already low dispersal species. There is therefore a good understanding of how ecological attributes of fishes can impact their neutral structure. With this knowledge in mind, we now turn to how environmental characteristics can influence adaptive structure.

4.2 | Adaptation with gene flow driven by ecological disturbance

All analyses—whether F_{ST} outlier or genotype–environment association—showed evidence for loci under selection despite the homogenizing influence of gene flow. For the genotype–environment associations, these included associations with key indicators of disturbance regimes: variation in run-off (i.e., flow) across years and perennality, the latter being the variation in run-off within a year. On the other hand, no associations were detected with average measures of run-off: average run-off across the year or average run-off for each season. This indicates that the variation in run-off, rather than the amount of run-off, is a key selective factor influencing the genetic variation of the species. This conclusion has major implications for large environmental flow management actions being planned and implemented within the MDB under the Basin Plan (<http://www.mdba.gov.au/basin-plan/whats-basin-plan>). Fish studies from other regions of the world have also reported on the influence of divergent selection along environmental gradients despite gene flow (e.g., Beheregaray & Sunnucks 2001; Saint-Laurent, Legault, & Bernatchez, 2003; Cooke, Chao, & Beheregaray, 2012a, 2012b), but we are unaware of fish studies that assessed the relative role of disturbance. Our survey of the golden perch suggests that ecological disturbance is a driving force of selection, and it may facilitate the resilience of populations in the face of future variability in hydroclimates (Barrett & Schluter, 2008; D'Odorico & Bhattachan, 2012; Palumbi, Barshis, Traylor-Knowles, & Bay, 2014; Tielbörger & Salguero-Gómez, 2014).

In addition, average annual temperature was associated with candidate adaptive loci, as expected given the known metabolic responses of fishes to temperature (McCairns, Smith, Sasaki, Bernatchez, & Beheregaray, 2016). These loci have the potential to allow resilience of populations under future expected increases in temperature and aridity in Australia. Associations of loci with rainfall were relatively minimal except with average coldest quarter rainfall, which is likely due to the high correlation of average coldest quarter rainfall with annual temperature (Table S3) rather than due to causation; nine of the 13 loci and two of the three loci that were associated with coldest quarter rainfall when including and excluding Paroo, respectively, were also associated with annual temperature. Similarly, an ecological genomics study of Murray cod found

temperature to be associated with adaptive divergence across the MDB (Harrison et al., in press). They also assessed one rainfall variable, precipitation seasonality, which showed adaptive divergence across the MDB but was also correlated with minimum temperature of the coldest month (Harrison et al., in press). While precipitation is a major selective agent of species worldwide (Siepielski et al., 2017), riverine flow seems to be more important for golden perch and potentially other flow-dependent freshwater fishes. This is because riverine flow influences their spawning and migratory timing (Reynolds, 1983), and rainfall and flow are poorly correlated in the MDB (Table S3) because flows are able to be derived from rainfall thousands of kilometres away.

The adaptive divergence in the MDB was predominantly associated with the Paroo River, with only 10 of the 31 loci remaining identified as candidate adaptive loci when this locality was removed. This is explainable by the Paroo River being environmentally extreme relative to the rest of the MDB; it is located closest to the arid centre of Australia, a region of exceptionally variable river flow and high temperatures (Figure 1). It is possible that there are other undetected adaptive divergences in the MDB or unknown complexities associated with the adaptive signal from the Paroo River as the power and sensitivity of an ecological genomics study is dependent on sampling design (Lotterhos & Whitlock, 2015) and the spatial configuration of the environmental landscape (Forester, Jones, Joost, Landguth, & Lasky, 2016). When nature is used as the laboratory, one is only able to use a study design that is realistic for the environmental landscape of interest and the resources available (Forester et al., 2016). Here, we believe the signal of adaptive divergence in the Paroo River is likely not a by-product of the neutral divergence of the Paroo River as its neutral divergence is quite low (maximum pairwise $F_{ST} = 0.024$) and also because our genotype-by-environment association analysis takes into account the potential influence of spatial structure (Guillot et al., 2014). The arid and flow variable environment of the Paroo River makes it perhaps the most representative of the future climate scenarios expected in the remainder of the system (Balcombe et al., 2011). Given the adaptively divergent variation harboured in the Paroo River and the ready ability for this variation to spread into the wider metapopulation, the Paroo River may be important to future persistence of golden perch throughout the MDB.

Our findings of flow variability as an ecological driver agrees with our previous study that showed perennality to be positively correlated with standing genetic variation of golden perch across three major basins based on microsatellite markers (Faulks et al., 2010b). While spring run-off across basins—a signal for spawning (Reynolds, 1983)—was also positively correlated with genetic variation in the previous study, this was not found in our current study, which may be due to the relatively low variation of spring run-off at a within-basin (i.e., MDB) scale. Our current findings contrast with the ecological genomic study of the southern pygmy perch in the MDB (Brauer et al., 2016). The pygmy perch showed low standing variation in fragmented populations and adaptive divergence linked to the narrow environmental range of remaining human-induced fragments. This is likely due to the pygmy perch's naturally low dispersal

capability and specialist attributes, which have already contributed to the need for rescue, captive breeding and subsequent re-introduction due to the human-exacerbated Millennium Drought of the population that inhabits the Lower Lakes (Attard, Brauer, et al., 2016, Attard, Möller, et al., 2016) and headwaters of the Murray River (Pearce, 2014). The contrasting findings of these two genomic studies align with the concept that high dispersal, ecologically generalist species have a greater capacity than low dispersal, specialist species to cope with ecological disturbances, whether natural or anthropogenic.

4.3 | Fat storage, stress and repair functions of candidate loci in variable environments

The functions of many of the annotated candidate loci have compelling connections to survival under ecological disturbance (Figure 5). Several of the candidate loci were enzymes involved in the metabolism of lipids—hepatic lipase (Dichek, Agrawal, Andaloussi, & Qian, 2006), bile salt-activated lipase (Hui, Hayakawa, & Oizumi, 1993) and neutral cholesterol ester hydrolase 1 (Sekiya, J-i, Igarashi, Okazaki, & Ishibashi, 2011)—and had allele frequency differences between the Paroo River and most of the remaining river system. Common garden experiments have shown local adaptation of fat storage in Atlantic silverside (*Menidia menidia*), with higher latitude populations adapted to high energy storage due to more severe winters (Schultz & Conover, 1997). The extreme hydroclimatic variability of the Paroo River relative to the remainder of the basin may require fish to be adapted to storing fat to survive during the many dry—and therefore low biological productivity (Leigh, Sheldon, Kingsford, & Arthington, 2010)—periods.

Other candidate adaptive loci appear to be involved in environmental stress responses related to temperature gradients across the MDB. One strong candidate was E3 ubiquitin-protein ligase RNF31. This enzyme binds to ubiquitin, a key protein involved in the digestion of protein damaged from environmentally induced stress, including temperature stress (Komander & Rape, 2010). Ubiquitin is upregulated in Antarctic fishes compared with species in temperate regions (Chen et al., 2008; Todgham, Hoaglund, & Hofmann, 2007), and its expression changes in fish that have been experimentally submitted to stressful conditions (Ryan, Pankhurst, & Wells, 1995; Tang & Lee, 2013), including elevated temperatures (Madeira, Madeira, Diniz, Cabral, & Vinagre, 2016). Heat shock proteins can also be involved in ubiquitination by presenting protein substrates to ubiquitin ligase (Esser, Alberti, & Höhfeld, 2004).

Remarkably, the particular ubiquitin ligase annotated here and another annotated candidate locus—tonsoku-like DNA repair protein (TONSL)—activate and inhibit, respectively, the same transcription factor (nuclear factor kappa enhancer binding protein, NF- κ B) (Iwai, Fujita, & Sasaki, 2014; Jacobs & Harrison, 1998; Ray, Zhang, Elias, & Ray, 1995). The specific potential adaptive role of the transcription factor is uncertain as it regulates a range of processes (Brasier, 2006; Correa et al., 2004; Gilmore, 2006; Perkins, 2007); however, the tonsoku-like DNA repair protein is known to maintain genome

integrity by repairing stalled or collapsed DNA replication forks (Duro et al., 2010; O'Donnell et al., 2010). Given the importance of ubiquitin in fishes under challenging environmental conditions, the known molecular association between the annotated ubiquitin ligase and another annotated locus (TONSL), and the clear allele frequency gradients across the MDB of these loci in association with environmental gradients, these loci are key candidates for local adaptation.

Lastly, we found candidate loci associated with tissue repair that had an allele frequency difference between the Lower Lakes and the remainder of the MDB. The Lower Lakes has lower summer and higher winter rainfall, lower variability in run-off and lower annual temperatures compared to the remainder of the basin. It was also highly affected by the Millennium Drought, which occurred from 1997 to early 2010 in south-east Australia (Van Dijk et al., 2013). There was therefore potentially selection from standing variation at loci associated with tissue repair to allow survival and recruitment in these environmentally divergent and, in the case of the drought, temporally changing conditions; rapid adaptation to a changing environment has also been found in other species (Bergland, Behrman, O'Brien, Schmidt, & Petrov, 2014; Therkildsen et al., 2013). Candidate loci that were successfully annotated were desmoglein-2, which is involved in structural adhesion of adjacent cells to each other and is upregulated during repair of fish fins (Padhi et al., 2004), and the von Willebrand factor, which is involved in blood clotting (Sadler, 1991) and is differentially expressed when fish are kept in crowded conditions that lead to wounding of fish (Christie, Marine, Fox, French, & Blouin, 2016). There were also differences in the allele frequencies of other candidate loci between the Darling River sample taken during the drought (i.e., 2002–2005) and after the drought (i.e., 2014), which suggests that selection from the drought may have also occurred elsewhere in the river system.

The allele frequency patterns at the candidate adaptive loci did not involve the alternate fixation of alleles, even at loci associated with the Paroo River (Figure 5). This is in line with numerous ecological genomic studies of fishes that suggest soft sweeps and polygenic adaptation, rather than hard sweeps, are the predominant mechanisms of local adaptation (reviewed in Bernatchez (2016)). Maintenance of both alleles in ecologically disturbed environments is also in line with expectations under temporally changing selective pressures, where the allele under selection may alternate over time and therefore an allele rarely becomes fixed (Bergland et al., 2014). In addition, loci that were associated with temperature gradients along the MDB, like the ubiquitin ligase and tonsoku-like DNA repair protein described above, would be expected to show and do show an allele frequency gradient rather than alternate fixation.

The most likely chance for long-term persistence of golden perch in the MDB given future predicted increases in aridity and flow variability is rapid adaptation from already available standing genetic variation. This is more likely to be successful if the necessary standing genetic variation has already been pretested in one of their metapopulation segments—such as in the hydrologically variable arid zone—which can then quickly spread elsewhere in the MDB through gene flow. The survival of golden perch in the Lower Lakes during

the anthropogenically exacerbated drought is a testament to the resilience of this fish to ecological disturbance. Temporal monitoring of adaptive allele frequency changes in the MDB could be conducted to allow an understanding of detected candidate loci associated with fat storage, stress and repair functions as they undergo selective pressures with future changes in environmental conditions (reviewed in Hansen, Olivieri, Waller, Nielsen, and The GeM Working Group 2012). In addition, comparative genomic monitoring between species with different life histories, such as high dispersal or generalist species like golden perch and low dispersal or specialist species, could confirm that life history attributes are key determinants of species extinction risk in future climates.

4.4 | Fishery management implications

Golden perch is recreationally fished throughout the MDB and commercially fished in the Lower Lakes, widely stocked in the river system and impoundments, and inhabits a dramatically human-altered environment due to, for example, in-stream structures to regulate river flow for agriculture. Despite this, existing management practices in addition to the generalist attributes and dispersal capabilities of golden perch have facilitated its persistence within the MDB, where many other fishes have declined to threatened status (Balcombe et al., 2011; Lintermans, 2013). Our findings support many current management practices but also highlight where management practices can be improved.

Our neutral and adaptive population structure findings suggest that the golden perch in the Lower Lakes and the Paroo River should be managed as separate stocks. Current practices already manage the Lower Lakes and fish in the lower Murray River as their own stock (Ferguson & Ye, 2012, 2016) based on findings of an early genetic study (Keenan, Watts, & Serafini, 1995). However, stocking is currently permitted from any Murray-Darling source into the northern Paroo River (under the management jurisdiction of the Australian state of Queensland) and no stocking is currently allowed in the southern Paroo River (under the jurisdiction of New South Wales (NSW)). Management practices should be altered so that, where permitted in the Paroo River, the river is only stocked using Paroo-sourced broodfish.

Golden perch stocking in the larger MDB is currently regionalized so that broodstock collected from a particular management zone are used to produce fingerlings that are released back into that zone (Gilligan, Beheregaray, Faulks, & Shaddick, 2009; NSW Department of Primary Industries 2010; Rowland & Tully, 2004). In doing so, the stocking follows typical genetic-based recommendations for stocking programmes (Ward, 2006), which would minimize the mixing of adaptively divergent fish. However, our current findings indicate that there is little adaptive divergence and no neutral divergence of fish in the larger MDB, and thus, we recommend for the separate stocks in the larger MDB to be amalgamated into one stock (with the Lower Lakes and the Paroo River kept as separate stocks). This would simplify management practices in the larger MDB and reduce required management resources. We do recommend though that the

Warrego River, which is a main river that runs parallel to the Paroo River (Figure 1) and was unsampled here, remains unstocked until a neutral and adaptive genetic assessment is conducted for that river system. The findings of high genetic connectivity in our study also suggest that fishways in the MDB are largely effective for golden perch; the fishways were built to allow large fish to move through in-stream structures (Baumgartner, Zampatti, Jones, Stuart, & Malen-Cooper, 2014).

We also confirmed that fish in impoundments are genetically similar to or indistinguishable from the localities in the open river system, including their genetic diversity, as previously suggested based on microsatellites (Faulks et al., 2010b). This is remarkably unlike many hatchery breeding programmes that show low diversity and genetic differentiation of captive reared and released fish (Araki & Schmid, 2010), and is perhaps due to the intermittent addition of new wild-caught golden perch to hatcheries (NSW Department of Primary Industries 2010; Rowland & Tully, 2004). However, we used the genomic data set to examine in greater depth the genetic structure and showed that the impoundments, especially Burrinjuck Dam, consisted of highly related individuals compared with the MDB river system. This explains the separation of some individuals in impoundments from the main clusters in the PCA and Bayesian assignment analyses: the separated individuals consist of related individuals. The presence of related individuals in impoundments may be due to the use of relatively few breeders in hatcheries, the skewed contribution of breeders to offspring or a combination of these. Such skewed contribution is commonplace in aquaculture (Brown et al., 2005; Liu et al., 2012; Loughnan et al., 2013). To minimize unnaturally high levels of relatedness, we recommend that fish for stocking should be sourced from more broodstock matings than the current minimum of five pairs (NSW Department of Primary Industries 2010).

In addition, there was no clear pattern to the allele frequency at adaptively divergent loci in impoundments (Figure 5). Reduced fitness of captive-born individuals in the wild is commonplace in stocking programmes (Araki & Schmid, 2010) and is particularly problematic if there is wild breeding between maladapted hatchery fish and wild fish (Kostow, 2009; Ward, 2006). Golden perch released to the natural river system have been shown to overwhelm in abundance the wild-born fish in some regions (Crook et al., 2016; Forbes et al., 2016), and so minimizing the interaction between wild and released captive-born fish would be an ideal management objective to reduce the genetic risk from stocking (Hindar, Ryman, & Utter, 1991; Kostow, 2009). Only stocking and allowing fishing in the isolated impoundments, as is conducted for silver perch (*Bidyanus bidyanus*) in the MDB (NSW Department of Primary Industries 2010), may be required in the future if demographic or genetic degradation of golden perch occurs in the river system. Due to the environmental variability and reproductive dynamics of golden perch in the MDB (see above section A *highly connected riverscape*), genomic monitoring of hatcheries, impoundments and the wild metapopulation, and environmental monitoring of the wild habitat, would be valuable to adaptively manage the system in the face of fishing, stocking and future climate change.

4.5 | Final remarks

The climate of Australia and regions elsewhere are expected to increase in aridity and temporal environmental variability, making standing genetic variation key to the persistence of species. Unlike low dispersal, specialist fishes, the high connectivity of golden perch in the MDB will probably allow locally adaptive traits found in relatively arid and hydrologically disturbed environments at the margin of the species' range to spread and be selected in localities that become ecologically disturbed in the future. We found that current fisheries management strategies have largely aided maintaining the natural genetic make-up of the species, but we recommend redesignation of some stocks based on the neutral and adaptive structure findings, refinement of hatchery practices to reduce relatedness levels in bred fish, and genomic, demographic and environmental monitoring of golden perch given likely future anthropogenic impacts. We have more broadly highlighted the influence of environmental heterogeneity, especially ecological disturbance, in shaping adaptive divergence and intraspecific biodiversity. Disturbance patterns are changing rapidly due to anthropogenic climate change, and understanding spatial and temporal patterns of genetic diversity can potentially allow us to predict the demographic response of populations to future climates and implement appropriate management strategies.

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DATA ACCESSIBILITY

SNP genotypes and reference sequences are available on Dryad: DRYAD entry <https://doi.org/10.5061/dryad.j24r0>. Locality coordinates and environmental data are in Table S2.

AUTHOR CONTRIBUTION

L.B.B. conceived the study. C.R.M.A. generated the data with contributions from all other authors, and analyzed the data with contributions from L.B.B., C.J.B. and J.S.-C. C.R.M.A. and L.B.B. co-drafted the article. All authors contributed to data interpretation and critically revised the article.

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