

A community-driven captive-breeding and reintroduction program maintains genetic diversity in a threatened freshwater fish

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Abstract

Collaborative approaches to conservation management are critical to respond to the ongoing biodiversity crisis. However, local community involvement in many conservation actions is lacking, especially within translocation and reintroduction programs. Similarly, rapid integration of genetic information into collaborative programs with local communities is rarely conducted. Here, we describe a community-based and collaborative reintroduction program for a threatened Australian freshwater fish, the southern pygmy perch (*Nannoperca australis*). We integrate on-the-ground translocation efforts by volunteers from local communities, captive breeding by a private aquarium business, and genetic analyses done by a research institution to provide a holistic framework for the reintroduction of southern pygmy perch. We evaluated genetic diversity, population structure, relatedness, and inbreeding across the duration of the reintroduction program using data from neutral and adaptive genomic markers. This allowed us to assess the ability of such a program to minimize inbreeding and retain genomic variation, and to promote adaptive potential of the reintroduced population. While genetic variation for the source populations was very low, we found no decrease in genetic diversity or increase in inbreeding across the program. These genetic findings support the efforts made by local communities and will further inform future reintroductions as part of a collaborative conservation framework. We expand on our empirical case study by describing a theoretical framework for integrating conservation genomics research with community-led conservation management programs and identifying the benefits of such a collaboration. Our study highlights the importance of multifaceted and integrated conservation management approaches to effectively protect and manage threatened species.

KEYWORDS

Australia, citizen science, conservation reintroductions, genetic rescue, population genomics

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1 | INTRODUCTION

Given the current state of the global extinction crisis (Ceballos et al., 2015), collaborative approaches between conservation scientists and non-expert community groups are required to effectively prevent species loss (Arletta et al., 2010; Chandra & Idrisova, 2011). Local community participation in conservation programs is mutually beneficial (Frigerio et al., 2018), significantly boosting conservation outcomes through communal investment, manual support, and local knowledge (Waylen et al., 2010). At the same time, collaborative conservation programs also provide gains in scientific literacy, fostered relationships and an increased use of scientific information in decision-making frameworks (Villaseñor et al., 2016). The integration of scientific and community institutions in conservation programs may also help bridge the *in situ* and *ex situ* management divide (Schwartz et al., 2017), including in captive-breeding and conservation reintroductions (Galbraith et al., 2016) and in the application of genetic data into conservation management (Taft et al., 2020). Despite these benefits and a growing number of collaborative conservation studies (Frigerio et al., 2018), there is a broad lack of public participation in conservation programs (Chandra & Idrisova, 2011), particularly within translocation and reintroduction actions (Galbraith et al., 2016). Similarly, few community collaboration programs incorporate genomic data to guide conservation actions such as translocations (Theobald et al., 2015).

Reintroduction programs are a critically important strategy for the conservation of rapidly declining and severely threatened species (Seddon et al., 2007), becoming increasingly necessary with escalating human development and anthropogenic climate change (He et al., 2016). The successful establishment of reintroduced populations remains challenging (Bubac et al., 2019) and is dependent on an array of factors, including environmental (Bellis et al., 2020), ecological (Harig & Fausch, 2002), demographic (Van Houtan et al., 2009), and genetic (Attard, Möller, et al., 2016; Furlan et al., 2020; Marshall et al., 2022; Seaborn et al., 2021) components, as well as longitudinal monitoring (Marshall et al., 2022). Of these, genetic diversity particularly does not often factor into the assessment of reintroduction success (Schwartz et al., 2007; Seaborn et al., 2021).

Maintenance of genetic variation in reintroduced populations preserves adaptive potential and allows populations to respond to current and future environmental changes (Brauer et al., 2017; DeWoody et al., 2021; Jamieson, 2011; Stange et al., 2021). However, genetic diversity can be readily lost throughout the captive-breeding and reintroduction process, driven by for example, founder effects in small broodstock populations (Witzenberger & Hochkirch, 2011), adaptation to captivity (Christie et al., 2012; Christie et al., 2016;

Williams & Hoffman, 2009) or unequal reproductive output (Gooley et al., 2018; Miller et al., 2009). These factors may impede on the ability for reintroduced populations to become established and persist in the wild, significantly impacting conservation management for the species (Willoughby et al., 2015). Despite the importance of estimating and maintaining genetic diversity within reintroduction programs, financial constraints and a lack of expertise within conservation managers is a significant barrier to its inclusion (Holderegger et al., 2019). Thus, cooperative projects between conservation geneticists and conservation practitioners—both professional and community-based—provide an exemplary approach to integrate genetic information with practical conservation management (Figure S1; Holderegger et al., 2019).

Freshwater species have experienced more rapid declines in abundance due to human impacts than terrestrial or marine species, as well as exceptionally high rates of extinctions (Barbarossa et al., 2021; Harrison et al., 2018). Small-bodied freshwater fishes are of particular risk to local or regional extirpation due to their poor dispersal ability, high habitat specialization, narrow endemism, and environmental stochasticity (Brauer & Beheregaray, 2020; Lintermans et al., 2020; Reynolds et al., 2005). Australian freshwater fishes, despite being one of the most threatened vertebrate groups (Garnett et al., 2022), receive relatively little legislative protection or management interventions (Lintermans et al., 2020). Thus, community collaborations are essential for the effective conservation of this highly imperiled group. Our collaborative reintroduction program focuses on the southern pygmy perch (*Nannoperca australis*): a small-bodied (<80 mm), weakly-dispersing and habitat-specialist freshwater fish endemic to south-eastern Australia. Southern pygmy perch prefer small streams and wetland habitats containing dense aquatic vegetation for shelter (Lintermans, 2007; Wedderburn et al., 2017) and show limited dispersal between river catchments (Brauer et al., 2016; Brauer & Beheregaray, 2020; Cole et al., 2016; Hammer et al., 2013). The expected lifespan is 3–6 years, with sexual maturation occurring after 1 year (Lintermans, 2007). The spawning season occurs annually, peaking from October to December, during which males develop contrasting black and red colors in the body and fins (Morrongiello et al., 2010). The species is distributed throughout the Murray-Darling Basin (MDB), coastal Victoria and northern Tasmanian rivers, with major intraspecific lineages corresponding with drainage basins (Buckley et al., 2021). Of these, the MDB lineage is particularly threatened due to habitat fragmentation, overextraction of water resources and the consequences of a widespread drought at the start of the millennium (Brauer et al., 2016; Brauer & Beheregaray, 2020; Hammer et al., 2013).

Owing to the combinations of threats impacting their persistence, southern pygmy perch are listed as

vulnerable or endangered under state and national protection acts, and near threatened in the IUCN red list (Beheregaray et al., 2021). Ongoing conservation efforts for the species have focused on the recovery of threatened populations, including a genetically-informed captive-breeding and reintroduction program for a formerly extirpated population from the lower MDB (Attard et al. 2016b; Marshall et al., 2022). In that region, captive-born descendants of wild-caught fish were reintroduced to the region between 2011 and 2012 (Hammer et al., 2013). The short generation time of the species enabled rapid assessment of reintroductions, with longitudinal monitoring of presence, abundance and fitness, as well as genetic sampling of multiple wild-born cohorts, attesting to the success of that reintroduction (Marshall et al., 2022). The local population showed low inbreeding and levels of genomic diversity similar to those found in the formerly extirpated population (Beheregaray et al., 2021). Despite these efforts, similar reintroduction programs have not been evaluated for other threatened populations within the MDB. This is particularly the case in headwater regions of the MDB, where southern pygmy perch is comprised of smaller and more isolated populations that show lower genetic diversity and higher extinction risk than populations in the lower MDB (Brauer et al., 2016; Brauer & Beheregaray, 2020; Cole et al., 2016).

In response to recent demographic declines and local extirpations of southern pygmy perch in headwater regions of the MDB (Brauer et al., 2016; Cole et al., 2016), a collaborative restoration program was established with the aim of reintroducing demographically viable populations

(Figure 1). This program is part of a broader Native Fish Recovery Plan (Mallen-Cooper et al., 2014) and the Tri-State Murray Natural Resource Management (NRM) Alliance “Magnificent Six” project, which sought to restore populations of threatened floodplain specialist fish species around the Murray River. A collaborative working group of local councils (City of Greater Bendigo), environmental groups (Friends of Crusoe and No. 7 Reservoir), natural resource agencies (North Central Catchment Management Authority), and fish hobbyist groups (Native Fish Australia, and the Australian and New Guinea Fishes Association) was established to source wild southern pygmy perch from the Avoca and Campaspe Rivers for captive-breeding at a nearby aquaculture facility (Middle Creek Farm). Volunteer participants from the fish hobbyist groups were heavily involved with the collection and transportation of wild-caught fish under the guidance of natural resource managers. The offspring of this breeding program were then used to establish multiple reintroduced populations in several wetlands near the source catchments, with releases performed by similar local volunteer organizations.

Here, we describe a community-driven captive-breeding and reintroduction program that includes genomic indicators of restoration success for southern pygmy perch in MDB headwater regions. We analyze genetic diversity, population structure, and reproductive output across three temporal cohorts (before capture, wild-caught broodstock and captive-bred F1s), and contrast these with a similar but independent reintroduction program in the lower MDB (Marshall et al., 2022). Our collaborative approach simultaneously bridges the in situ

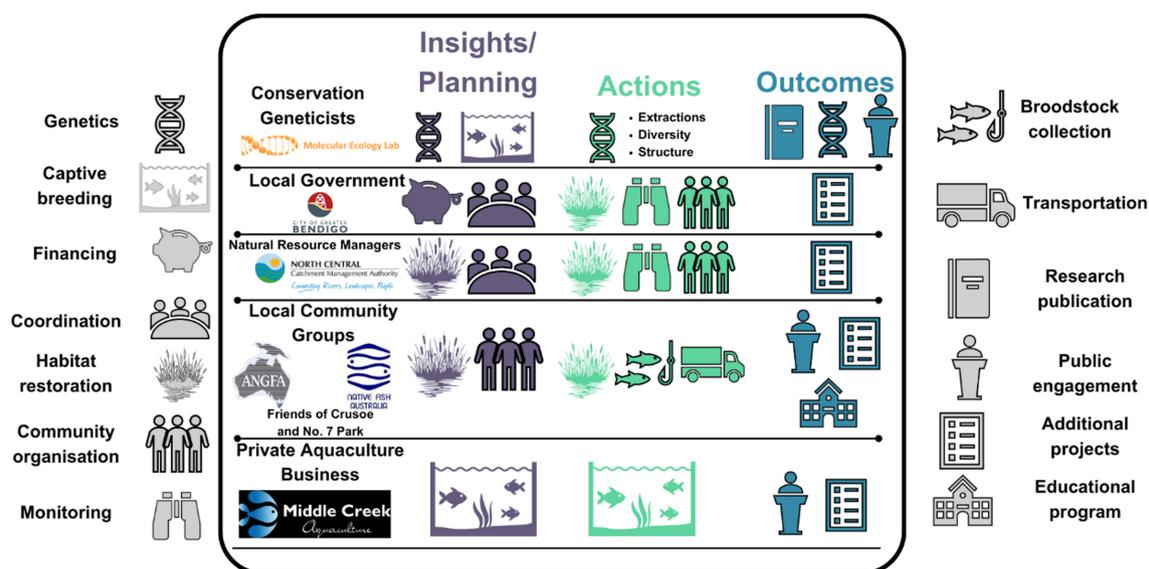


FIGURE 1 The collaborative conservation program for the reintroduction of southern pygmy perch in the Bendigo region of Victoria, Australia. Each line describes how each partner was involved in the planning (left column; purple) and implementation (middle column; green) of the reintroduction program, as well as their specific relevant outcomes (right column; blue).

and ex situ management divide (Schwartz et al., 2017) as well as the gap between conservation managers and academic researchers (Holderegger et al., 2019). We leverage on-the-ground translocation efforts by local communities, captive breeding by aquarium industry and genetic analyses conducted by a research institution to provide a holistic framework for the reintroduction of a threatened species.

2 | METHODS

2.1 | Establishing community collaboration and preparing reintroduction sites

Formed in 2015, the “Tri-State Murray NRM Alliance” comprises six regional bodies and aims to “grow local economy, secure the environment, and motivate the community” along the Murray River (Tri-State Murray NRM Regional Alliance, 2016). Key among these aims was the development of the “Magnificent Six” project, which aimed to recover populations and prevent extinctions of six, small native fish species (including southern pygmy perch) through habitat recovery and translocation efforts. In 2018, a partnership between the North Central Catchment Management Authority, City of Greater Bendigo Council, Native Fish Australia (NFA) and the Australian and New Guinea Fishes Association (ANGFA) was established to secure wild populations of southern pygmy perch from catchments within the Bendigo region, captive breed broodstock, and translocate offspring into nearby restored surrogate or formerly occupied habitats. Suitable source populations were identified based on prior knowledge of population genetic structure (Brauer et al., 2016; Cole et al., 2016), including the Avoca River, and McIvor and Jew’ Harp Creeks in the Campaspe River catchment (Figure 2, Sites 3–5). Translocation sites were surveyed using fyke nets prior to release, to ensure that the invasive predator redfin perch (*Perca fluviatilis*) and carp (*Cyprinus carpio*) were not present, and to confirm the current absence of southern pygmy perch (Mallen-Cooper et al., 2014). The City of Greater Bendigo and the Friends of Crusoe and No. 7 Reservoir group further prepared the release sites through extensive aquatic vegetation planting and woody habitat installation to generate suitable micro-habitat for the translocated pygmy perch.

2.2 | Captive breeding and reintroduction program

Wild-caught fish from the three sites (Figure 2, Sites 3–5) were collected by volunteer community members from NFA and ANGFA under the guidance of natural resource

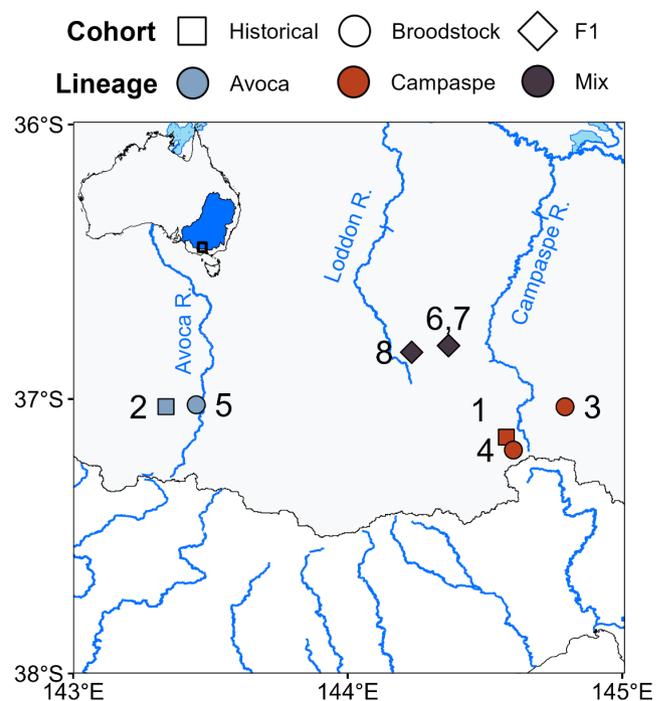
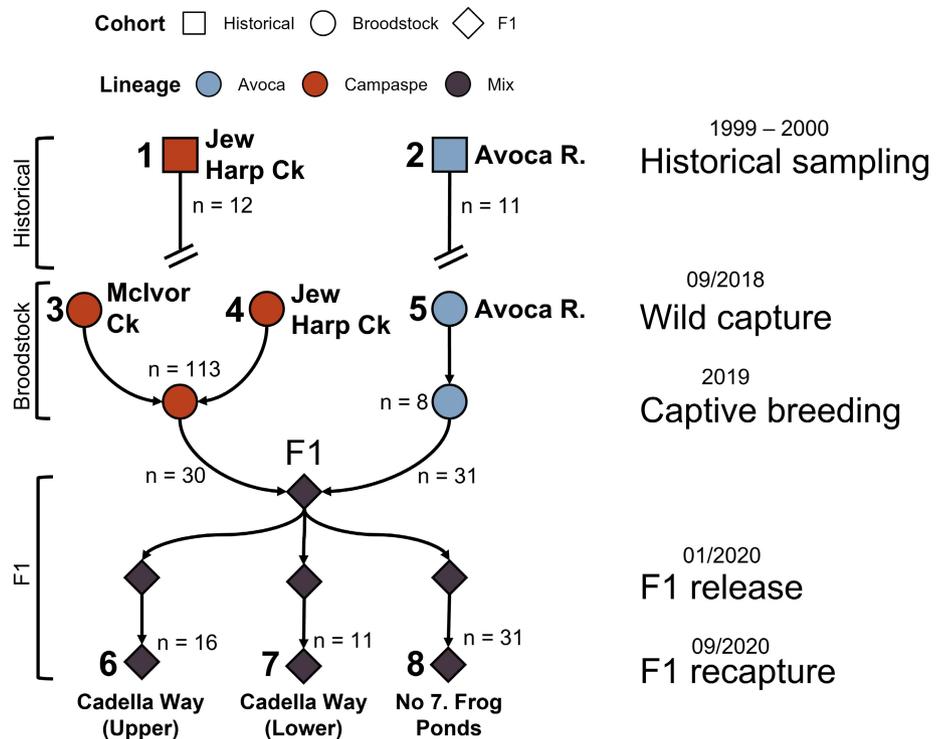


FIGURE 2 Map of sampling region and study sites. Shapes indicate temporal cohorts while colors indicate spatial genetic populations (based on Brauer et al., 2016). Black lines indicate major drainage divides. Inset depicts study extent, with the Murray-Darling Basin highlighted in blue.

managers in late 2018 to be used as broodstock for the breeding program (Figure 3; $n = 121$). Given that only males were collected from McIvor Creek, and that previous research suggested they likely belonged to the same genetic population as those from Jew Harp Creek (Brauer et al., 2016), these individuals were pooled prior to breeding (Figure 3) and subsequently referred to as the Campaspe lineage. We used prior knowledge about captive breeding of southern pygmy perch (Attard et al. 2016b) to make recommendations around the design of the captive breeding groups. These recommendations included the minimum number of fish to be used as broodstock (Attard et al. 2016a), the sourcing of wild-caught fish to account for population uniqueness (Brauer et al., 2016; Cole et al., 2016), and minimizing the duration of captive-breeding to avoid adaptation to captivity (Brown & Day, 2002; Witzemberger & Hochkirch, 2011).

The two lineages were then captive-bred at Middle Creek Farm in 2019, with the resultant F1 offspring being released across three nearby sites (Figure 2, Sites 6–8) in early 2020. These lineages were bred separately to maximize the retention of their respective unique genetic diversity, given unequal numbers of broodstock fish collected. At each of these sites (Sites 6–8), a total of 175 Campaspe and

FIGURE 3 Timeline of wild capture, captive breeding, and reintroduction program. Arrows depict the movement of individuals across sites and cohorts. Symbols and numbers relate to sites shown in Figure 2. The number of genetic samples collected at each site is indicated by n —released F1 offspring samples were collected prior to pooling for release.



25 Avoca F1s were released, with similar releases occurring across other unsampled sites (not shown). These additional sites were not surveyed due to logistical constraints. A subset of released offspring was sampled for genetic analysis prior to release ($n = 61$). Adult fish in these three sites (Figure 2, Sites 6–8) were recaptured in late 2020, representing the surviving F1 offspring ($n = 59$). Additionally, we included historical samples for the Avoca and Jew Harp Creek populations ($n = 23$; total n across all cohorts = 256). These samples were previously sequenced as part of a broader landscape genomics project (Brauer et al., 2016) and sourced from museum tissue originally collected from 1999 to 2000 (Figure 2, Sites 1–2). Across all contemporary sampling periods, fish were fin clipped, measured (body length and sex), and returned live to their respective collection sites. Fin tissue was preserved in 100% ethanol and stored at -80°C until DNA extraction.

Additionally, we obtained previously sequenced genomic data ($n = 271$) from a similar but independent reintroduction program that was conducted in the lower MDB (Marshall et al., 2022). That included wild-caught broodstock, two generations of captively-bred offspring (F1 and F2), six consecutive generations following a reintroduced population, and a single generation of three neighboring wild populations (Table S1). This data were used to contextualize genetic diversity estimates for our collaborative reintroduction program in the upper MDB.

2.3 | DNA extraction, genomic libraries, and sequencing

DNA was extracted using a modified salting out process (Sunnucks & Hales, 1996). Genomic DNA quality was checked using a spectrophotometer (NanoDrop, Thermo Scientific), agarose gels, and a fluorometer (Qubit, Life Technologies). Double-digest restriction site associated DNA (ddRAD) libraries were created in-house using the restriction enzymes *Sbf1* and *Mse1* in a modified ddRAD protocol (Brauer et al., 2016; Peterson et al., 2012), with 150 bp reads paired-end sequenced on a HiSeq 4000.

All sequences—including previously-sequenced historical and lower MDB samples—were demultiplexed using the dDocent pipeline (Puritz et al., 2014). Trimmed reads were aligned and mapped to a recently assembled, chromosome-level reference genome for southern pygmy perch (under preparation) using bowtie2 (Langmead & Salzberg, 2012). Single nucleotide polymorphisms (SNPs) were called across all sequences together using dDocent and filtered using VCFTools (Danecek et al., 2011; full filtering pipeline described in Table S2). Called SNPs were further filtered by removing co-varying loci with a variance inflation factor >5 to account for linkage disequilibrium. A dataset of adaptive SNPs was amassed by selecting candidate adaptive SNPs previously associated with hydroclimatic variation across the MDB (details in Brauer et al., 2016). These SNPs were removed from the global SNP dataset to form the putatively neutral global dataset. Each of these two datasets were

further subdivided into separate reintroduction programs (either the lower MDB program detailed in Marshall et al. (2022) or the upper MDB program described here) for further evaluation. As some global SNPs may be monomorphic within each respective reintroduction program, monomorphic sites were removed from each subset.

2.4 | Genetic diversity

Genetic diversity measures (number of alleles, N_a ; percentage of polymorphic loci, %poly; observed and expected heterozygosity, H_o and H_e ; and individual inbreeding coefficient, F) were calculated for each population and cohort using the R packages *Adegenet* (Jombart, 2008) and *Hierfstat* (Goudet, 2005). All measures were calculated using the global neutral and adaptive datasets.

2.5 | Population structure

Population structure across the upper MDB reintroduction program was assessed using principal coordinates analyses (PCoA) in *DartR* (Gruber et al., 2018) and both neutral and adaptive SNPs, separately. We also estimated population structure of both SNP datasets using unsupervised models in *Admixture* (Alexander et al., 2009), excluding the historical cohorts to better resolve broodstock and offspring relationships. For all *Admixture* analyses, we estimated the most suitable number of populations (K) using a 10-fold cross-validation procedure (Alexander & Lange, 2011). All other parameters were kept at default values.

2.6 | Relatedness, parentage, and reproductive output

Pairwise relatedness within each population was estimated using the triadic likelihood relatedness estimator (r ; Wang, 2007) in *Related* (Pew et al., 2015) and a genotype error rate of 0.02. We assigned F1 offspring to wild-caught parents using *Snppit* (Anderson, 2012) and the triadic likelihood estimator in *Sequoia* (Huisman, 2017). As recommended to improve parentage assignment (Huisman, 2019), we first filtered SNPs to only those present in all individuals and with a minor allele frequency >0.05 (3016 SNPs). We assumed a genotype error rate of 0.015 based on our sequencing replicates and discrete (non-overlapping) generations. This dataset was used in *Sequoia*. Due to computational limitations, we further subsampled this dataset to 500 SNPs for *Snppit*. All other parameters were kept at default values. The reproductive output of parents was

calculated using the number of inferred offspring per parent based on assignments made with both methods.

3 | RESULTS

3.1 | Community involvement

Local community volunteers were involved across all stages of the project. Eight volunteers, recruited through ANGFA and NFA, spent approximately 16 h (plus travel) setting up nets and catching fish as part of the initial DNA collection. This group expanded to 12 volunteers for the collection of broodstock for the captive breeding program, contributing approximately 24 h of time across several consecutive days to set nets, collect fish and transport broodstock to Middle Creek Farm. Within the captive breeding program, community volunteers contributed a total of 270 h over 24 weeks for broodstock care and conditioning, and growing fry. Six volunteers were then involved in the release of captive-bred juveniles, contributing 8 h of time (plus travel). Without these significant contributions of labor, a reintroduction program of this scale would not have been possible.

3.2 | Bioinformatics

A total of 1,655,079 raw SNPs were obtained, with 19,136 high-quality global SNPs across all 596 individuals retained after filtering (Table S2; Figure S2). These SNPs were separated into 18,916 putatively neutral and 247 putatively adaptive global SNP datasets. Subdividing datasets into each reintroduction program with monomorphic SNPs removed resulted in 17,216 neutral and 235 adaptive SNPs for the lower MDB program and 8509 neutral and 100 adaptive SNPs for the upper MDB program. For the admixture analysis of the upper MDB program, removing historical samples resulted in 8378 neutral and 100 adaptive polymorphic SNPs.

3.3 | Genetic diversity

All measures of genetic diversity, across both neutral and adaptive datasets, were considerably higher within the lower MDB program than in the upper MDB (Figure 4). All upper MDB populations retained similar levels of diversity across neutral and adaptive datasets, with marginally but consistently higher diversity in the Avoca lineage than the Campaspe lineage across all cohorts. Inbreeding coefficients tended to be low overall but greater within Campaspe broodstock and F1s than their

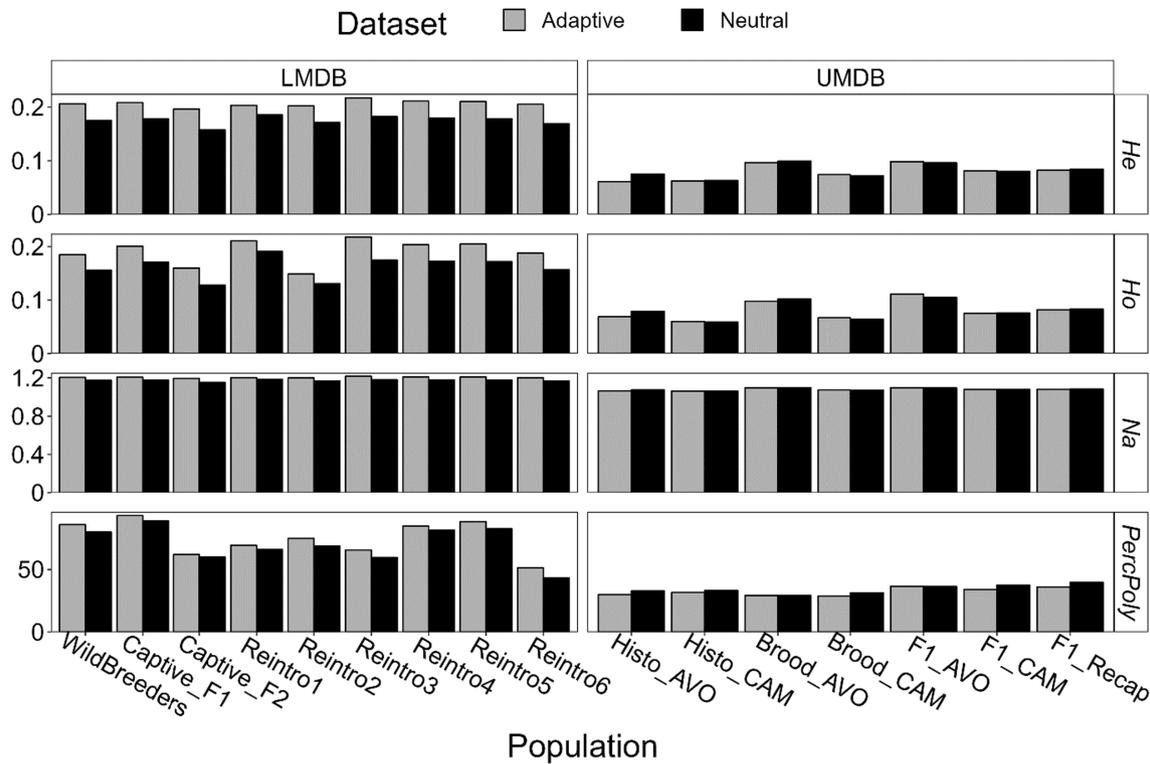


FIGURE 4 Measures of genetic diversity per population based on 247 global adaptive (gray) and 18,916 global neutral (black) SNPs, across the lower MDB reintroduction program (left; Marshall et al., 2022) and the upper MDB reintroduction program (right). Populations are arranged in chronological order, with the oldest cohorts on the left. He = mean expected heterozygosity; Ho = mean observed heterozygosity; Na = mean number of alleles; PercPoly = mean percentage of SNPs polymorphic. MDB, Murray-Darling basin; SNP, Single nucleotide polymorphism.

Avoca counterparts, except in the historical cohorts (Figure S3). The recaptured population had levels of genetic diversity more similar to Campaspe populations and a wide distribution of inbreeding coefficients.

3.4 | Population structure

Population structure across the upper MDB reintroduction datasets related more strongly to spatial than temporal structure, with the first PCoA axis separating Avoca and Campaspe lineages, and the second axis separating two broodstock clusters within the Campaspe lineage (representing the two sample sites; Figure 5). Some temporal population structure was evident between historical and contemporaneous cohorts within each lineage, which was more apparent within the neutral dataset (Figure 5a). Intermediate clusters were apparent within the F1 generations, likely representing hybrid individuals between the three broodstock populations. Similarly, admixture supported the same three clusters related to spatial structure (Figure S4), with several hybrid F1s spread across all three offspring cohorts in both datasets (Figure 5c). Two Avoca F1s were identified as Avoca x Campaspe hybrids, despite their

separated breeding groups. A single Campaspe F1 was identified as a mislabeled Avoca F1. Only two (3.5%) recaptured F1 individuals had Avoca ancestry, with all others either Jew Harp Creek offspring ($n = 39$; 68.42%) or hybrids from Jew Harp Creek and McIvor Creek parents ($n = 16$; 28.07%).

3.5 | Relatedness and reproductive output

Pairwise relatedness was low across all populations, with $r < 0.2$ for almost all historical and broodstock samples (Figure 6). Overall relatedness was slightly higher within the Avoca than the Campaspe offspring, with an increase in the recaptured F1 population. Parentage assignments made using both approaches suggested identical parent-offspring triads, with both parents successfully assigned to 22 Campaspe (73.33%), 29 Avoca (93.55%), and 33 recaptured (57.89%) F1 offspring across both methods (Table S3). An additional 16 parent-offspring triads which were not detected with *Sequoia* were detected using *Snppit*. An additional six Campaspe (20%) and 21 recaptured (36.84%) F1 offspring had a single parent assigned using *Sequoia* (Table S4). Reproductive output was not

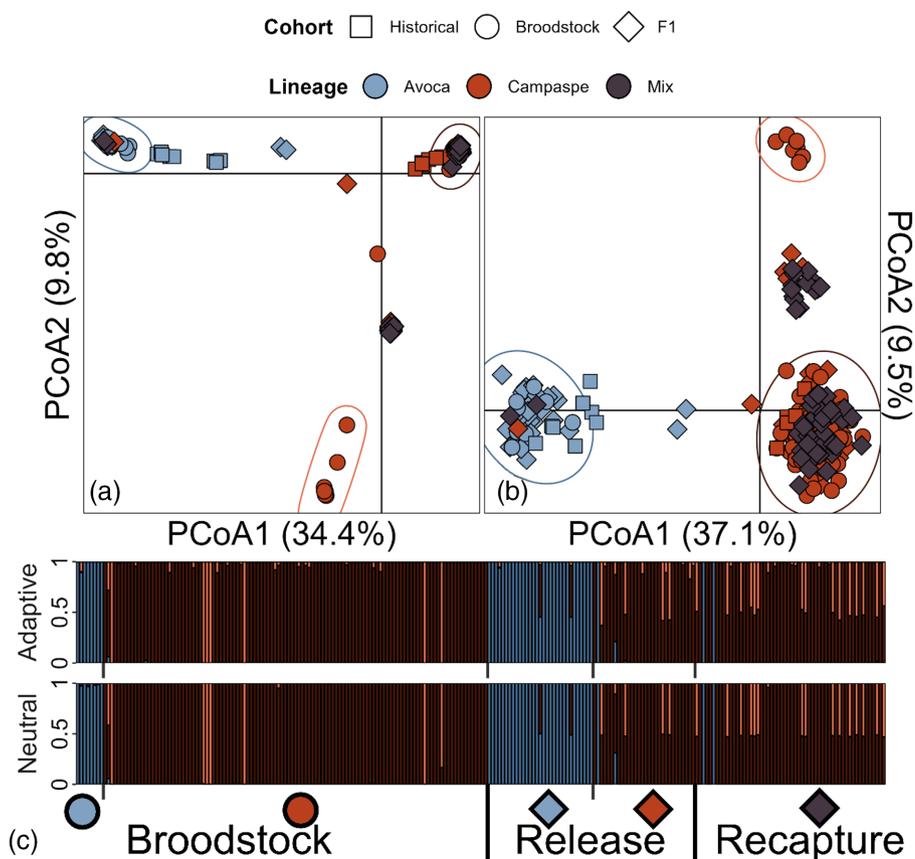


FIGURE 5 Population structure of upper MDB populations using two approaches. Principal coordinate analyses based on (a) 8509 putatively neutral, and (b) 100 putatively adaptive SNPs, with cohorts indicated by point shapes and source populations indicated by colors. Ellipses define individuals with >80% assignment to a cluster in admixture. (c) Admixture plots for contemporary upper MDB individuals using $K = 3$ clusters, based on 100 putatively adaptive (top) and 8378 putatively neutral (bottom) SNPs. Each column represents a single individual, with colors indicating assignment probability to a given cluster. Population labels are shared with the PCoA plot. SNP, Single nucleotide polymorphism.

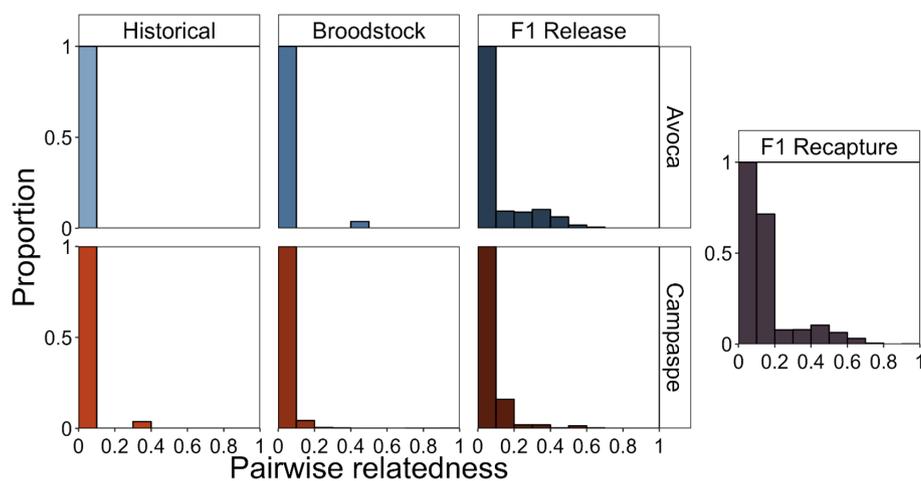


FIGURE 6 Histograms of pairwise relatedness for upper MDB populations. Populations are arranged in chronological order. MDB, Murray-Darling basin.

skewed in the Campaspe population, with most inferred parents not individually contributing many offspring (mean = 1.82 offspring per parent). Contrastingly, reproductive output was more variable across Avoca parents (2–20; mean = 8 offspring per parent; Figure S5).

4 | DISCUSSION

Collaborative approaches between conservation geneticists and local communities provide a strong data-driven

approach to time-sensitive conservation management of threatened species. Small-bodied freshwater fishes often have short generation times and are at great risk of losing genomic diversity and becoming locally extirpated due to human impacts. At the same time, they exemplify a study system to rapidly document the benefits of community efforts in conservation reintroductions. Our captive-breeding and reintroduction program for southern pygmy perch successfully maintained genetic diversity and avoided inbreeding despite the very low diversity of source populations. The rapid response offered by

community involvement in the program, combined with insights presented by genomic data, provides an effective and practical management approach to their ongoing conservation.

4.1 | Genetic components of reintroduction and management

All upper MDB populations demonstrated extremely low genetic diversity, with approximately half the diversity of lower MDB populations. This finding is consistent with other population genomics studies on the species, which demonstrated lower genetic diversity in upland southern pygmy perch populations (Brauer et al., 2016; Brauer & Beheregaray, 2020; Cole et al., 2016). The levels of genetic diversity observed here are lower than other threatened freshwater fishes (e.g., Biesack et al., 2020; Kajungiro et al., 2019; Skovrind et al., 2016), highlighting the conservation concern for these populations. Relatedly, population-level fitness is often correlated with measures of heterozygosity (Chapman et al., 2009; Kardos et al., 2021; Paige, 2010). This is especially a concern for reintroduced populations as genetic erosion following translocation (e.g., Mueller et al., 2022; Ottewell et al., 2014; Thavornkanlapachai et al., 2021) is often thought to reduce the likelihood of establishment (Schäfer et al., 2020; Willoughby et al., 2015).

Despite a lack of a priori information on the genetic diversity of headwater populations, both genome-wide and adaptive diversity were effectively maintained with minimal inbreeding. Reproductive output was not strongly biased by overrepresentation of few parents, minimizing the loss of genetic diversity that can occur in captive-bred populations (Gooley et al., 2018; Witzemberger & Hochkirch, 2011). Additionally, a higher proportion of the recaptured population were hybrids (~28%, compared to 6.45% and 16.67% of released Avoca and Campaspe cohorts, respectively), potentially suggesting that genetic mixing may improve individual survivability. The higher levels of hybridization in F1 cohorts likely contributed to the maintenance of heterozygosity, as reintroduced populations from mixed sources may have moderately higher heterozygosity than their respective source populations (Huff et al., 2010; McKnight et al., 2023). While genetic mixing may result in the loss of unique genetic variation from the source populations due to homogenization, the low genetic diversity of—and strong genetic drift and limited adaptive differentiation between—upland populations (Brauer et al., 2016) suggests that mixing is a more effective conservation strategy than maintaining genetic “uniqueness” (Ralls et al., 2018; Weeks et al., 2016). Together, these findings indicate that the conservation

approaches conducted by local communities did not compromise genetic diversity.

4.2 | Community engagement and collaborative conservation

Although community involvement in conservation management has increased in recent years (Frigerio et al., 2018), examples of collaborative approaches between conservation geneticists and local communities are relatively scarce (Galbraith et al., 2016; Holderegger et al., 2019). As a result, few citizen science programs incorporate measures of genetic diversity (2%; Theobald et al., 2015). Our study highlights the increased conservation value of a collaborative approach between conservation geneticists and diverse community groups in the reintroduction of a threatened fish. We reiterate claims made elsewhere (e.g., Galbraith et al., 2016; Parker, 2008) that community involvement within translocation programs is critical for their success and provide strong conservation advocacy to a wide audience.

For reintroduction programs, strong community engagement can significantly improve conservation outcomes through the provision of large quantities of data, particularly regarding local knowledge (Kadykalo et al., 2021), expanded spatial and temporal scope (Loss et al., 2015; Theobald et al., 2015), and the additional work force without substantial financial cost (MacPhail & Colla, 2020; Waylen et al., 2010). Here, local communities were directly involved in the design and implementation of the reintroduction program, including the collection and transportation of broodstock (ANGFA and NFA) and the restoration and preparation of suitable release site habitat (Friends of Crusoe & No. 7 Reservoir). These efforts played a critical role in the effectiveness of the reintroduction program: subsequent monitoring at the two Cadella Way wetlands release sites (Sites 7 and 8, Figure 2) in 2021 and 2022 detected large numbers of southern pygmy perch (>300 fish per site), with an abundance of new recruits (~95% of all captures; unpublished data). The success of the reintroduction has garnered significant positive responses from community members, elevated social media engagement with volunteer organizations (ANGFA and NFA) and a series of public presentations documenting the program. Furthermore, NFA have since established an educational program using aquariums with southern pygmy perch in local schools: these are used to teach students about the importance of protecting native fishes, the impacts of pest species and basic water chemistry. Based on these outcomes, similar collaborative programs have been developed within the region: an additional seven landcare groups and over 20 individual landholders have been incorporated into new and ongoing reintroduction

programs in response. Together, these actions demonstrate not only positive conservation outcomes for a threatened freshwater fish, but the immediate benefits of community inclusion for outreach and education.

4.3 | Expanding collaborations for conservation management

Collaborative conservation approaches comprised of local communities, conservation managers, government-based institutions and professional scientists provide a strong framework for ongoing species management (Gavin et al., 2018; Theobald et al., 2015). Volunteer-based monitoring can provide long-term temporal trends in reintroduction programs, which can be further assessed, informed and guided by local-scale environmental management and insights from genetic analysis by professional scientists (Berkes, 2004; Holderegger et al., 2019). However, integrating conservation genetics theory and insights into collaborative management frameworks remains a challenge (Theobald et al., 2015). A significant barrier to this inclusion is the difficulty of translating complex genetic concepts and insights into clear and transparent management actions for practitioners (Britt et al., 2018; Holderegger et al., 2019). Our research highlights some of the key metrics (neutral and adaptive diversity; admixture; reproductive output) by which we can evaluate reintroduction success using genetic information and apply this knowledge to conservation management (reviewed in Hohenlohe et al., 2021). These metrics align with recent suggestions for genetic monitoring of threatened (Hoban et al., 2021) and translocated (Van Rossum & Hardy, 2020) populations. Although these metrics may not directly relate to local community aims in restoration projects, conservation genetics perspectives are also intrinsically linked to the broader goal of maintaining stable populations and preventing local extinction (Figure S1). By including conservation geneticists within a formalized co-management framework (Trimble & Plummer, 2019), critical components of population sustainability such as adaptive potential and inbreeding depression can be better understood and managed (DeWoody et al., 2021; Holderegger et al., 2019). Within the context of our reintroduction program, ongoing genetic monitoring facilitated by local communities would allow for the detection of genetic erosion (e.g., Mueller et al., 2022; Thavornkanlapachai et al., 2021) and determining whether further genetic mixing is recommended (Fitzpatrick et al., 2023). Thus, we advocate for stronger and formalized collaborative frameworks between conservation geneticists, local communities and government bodies to provide robust

and integrated management strategies which could be continually improved through iterative learning (Britt et al., 2018; Trimble & Plummer, 2019).

4.4 | Conclusions and conservation implications

Our large-scale collaboration spanning volunteer community groups, local government, natural resource managers, and conservation geneticists resulted in the successful reintroduction of several locally extirpated freshwater fish populations. Although genetic diversity for the populations was extremely low—even relative to other imperiled populations of the species—it was effectively maintained across captured, released, and recaptured populations without an increase in inbreeding. Local volunteer communities are vital for the species ongoing management, organizational oversight and further assessment of genetic diversity and inbreeding to provide a holistic and effective long-term management plan for these populations.

AUTHOR CONTRIBUTIONS

Sean James Buckley contributed to all sections of data analysis and drafting of the manuscript. Luciano B. Beheregaray designed and supervised the study, obtained resources, and helped with manuscript drafting. Diana-Elena Vornicu collated and extracted the DNA and generated the genomic libraries for sequencing. Chris Brauer generated the genotype data. Chris Lamin and Peter Rose performed the captive breeding and organized reintroduction events. All authors contributed to interpretation of results and critically revised the manuscript. Our study brings together a diversity of relevant stakeholders and includes authors representative of land-care management and private enterprise. The study design and implementation were developed through discussion with relevant stakeholders throughout the project. Our findings were communicated to all members of the collaboration throughout the project and have already formed the basis for further cooperative reintroduction efforts in other catchments.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data will be made available on FigShare upon acceptance.

ETHICS STATEMENT

Collection of samples were carried out in accordance with relevant guidelines and regulations of Australia and under approval of Flinders University Animal Welfare Committee.

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SUPPORTING INFORMATION

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

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