



RESEARCH ARTICLE

Assessing the benefits and risks of translocations in depauperate species: A theoretical framework with an empirical validation

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Abstract

1. Conservation translocations are becoming more common to assist in the management of threatened native species. While many translocation programs focus on maximizing survival in newly established populations, consideration is also required for the persistence of source populations.
2. Here, we present and test a theoretical framework that assesses the translocation trade-off between increasing a species probability of survival and decreasing a species' overall genetic diversity. We anticipate that (a) the genetic diversity of translocated populations will be reduced compared to the source due to a failure to capture and retain genetic diversity and (b) the genetic diversity of the source population will decline due to the removal of founder individuals.
3. We test this framework with an empirical study of redbfin blue eye *Scaturiginichthys vermeilipinnis*, a critically endangered fish species which has undergone several replicate translocations, established with founders sourced from a single remnant population. Several generations after reintroduction, we show that the predicted survival of the species has improved as a result of these translocations.
4. While the species' genetic diversity has been retained across all populations combined (translocated and source), we show that genetic diversity in each individual population (including the source) is reduced compared to the source population prior to translocation.
5. *Synthesis and applications.* Conservation translocations can provide great benefits to species survival, enabling extinction risk to be spread across multiple populations. Translocated populations, however, often harbour reduced genetic diversity compared to source populations and initiating translocated populations can decrease the genetic diversity of source populations, placing them at an increased risk of extinction. The framework presented here enables the trade-off between extinction risk and retention of genetic diversity to be established. This will

enable the optimal conservation strategy to be employed to increase the long-term persistence and evolutionary potential of a species.

KEYWORDS

conservation translocation, endangered species, extinction risk, genetic diversity, redbfin blue eye, reintroduction, translocated population

1 | INTRODUCTION

Conservation translocations involve the deliberate movement of individuals from one location with release into another, with the aim of maintaining biodiversity and ecosystem function (IUCN & SSC, 2013). With biodiversity being lost at a remarkable rate, conservation translocations are becoming an increasingly important tool for wildlife management, particularly for small, isolated populations where stochastic factors can increase extinction risk (Lande, 1998). Conservation translocations provide an opportunity to free species from immediate threats such as predation, disease and habitat loss (Ceballos et al., 2015; Thomas, 2011).

The overall survival of a species will be influenced by the persistence of populations on individual habitat patches and by migration rates among patches. This includes both translocated populations and source populations. The persistence of these individual populations is, in turn, influenced by both demographic and genetic factors (Woodruff, 1990). Despite this, population dynamics and population genetics are rarely considered collectively (Clarke & Young, 2000; Robert, Couvet, & Sarrazin, 2007), while the survival and genetic health of source populations remain an essential, but often overlooked part of translocation projects (Armstrong & Seddon, 2008; George et al., 2009). In many cases, the effect of genetic and demographic factors on source and translocated populations can act antagonistically.

While there are some noteworthy translocation success stories (Bangs & Fritts, 1996; Boyd, 2003; Taylor, Jamieson, & Armstrong, 2005; Weeks et al., 2017), many translocation attempts fail (Fischer & Lindenmayer, 2000; Germano & Bishop, 2009; Griffith, Scott, Carpenter, & Reed, 1989; Wolf, Griffith, Reed, & Temple, 1996). The impacts of failed translocations extend to source populations, where the removal of founder individuals and their associated genetic content will likely have a detrimental effect (IUCN & SSC, 2013). For some species, the number and census size of remnant populations from which to source founders may be limited, meaning that attempts to initiate new populations will likely have an even greater impact. To achieve the best conservation outcome for a species, the potential benefits of translocations for new and existing populations need to be weighed against the potential risks. In some cases, conservation effort may be best focused on improving the survival of remnant populations while, in other cases, taking no action may be the less risky option (IUCN & SSC, 2013). In this study, we outline the risks and benefits of translocations on population demographics and genetics for both the source and recipient populations.

1.1 | Population demographics

Translocations can take on one of three forms, with individuals relocated to either (a) a site previously occupied by the species, that is a reintroduction, (b) a site from which the species has never been recorded, that is an introduction or (c) a site where the species currently exists, but often in low numbers or with reduced genetic diversity, that is augmentation or supplementation. The criteria for translocation 'success' vary, but generally necessitate the persistence of founder individuals and (for the first two forms) sufficient breeding to establish a self-sustaining population across multiple generations (IUCN & SSC, 2013). Translocations have proven to be a key conservation tool as they can dramatically improve the probability of survival for a variety of species (Bangs & Fritts, 1996; Boyd, 2003; Miskelly & Powlesland, 2013; Taylor et al., 2005). However, a range of site-specific, species-specific and individual-specific factors contribute to a high failure rate among reintroductions or introductions (Fischer & Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996). These include the presence of known threats, limited opportunity for population growth and gene flow, lack of climatic and ecosystem suitability, individual behavioural and population dynamics, as well as, the physiological stress resulting from transfer (Cochran-Biederman, Wyman, French, & Loppnow, 2015; Fischer & Lindenmayer, 2000; Gaston, 2009; Ricciardi & Simberloff, 2009). The number of founders required for translocation success varies greatly but the likelihood of translocation success typically increases as the number of founders increases and the number of translocation attempts increases (Ahlroth, Alatalo, Holopainen, Kumpulainen, & Suhonen, 2003; Fischer & Lindenmayer, 2000). To determine whether translocations will provide an overall benefit to a species' viability, consideration must be given to the initial survival probability of remnant populations, the probability of translocated populations establishing and the cost of founder removal on the remnant populations.

1.2 | Population genetics

Genetic factors also play a critical role in the success and viability of translocated populations. Low levels of genetic diversity can lead to inbreeding depression and reduced fitness in the short term (Frankham, Bradshaw, & Brook, 2014; Lande, 1998) and reduce long-term evolutionary potential (Spielman, Brook, & Frankham, 2004). Introduced or reintroduced populations will typically harbour reduced genetic diversity compared to source

populations due to (a) failure of the founders to capture the complete diversity of the source and (b) failure to retain the genetic diversity of the founders through unequal breeding contributions and genetic drift. Genetic drift can lead to differentiation between populations and rapidly deteriorate genetic diversity, contributing to reduced fitness and increased inbreeding (Lande, 1998). For populations translocated to small, isolated habitats, ongoing gene flow will likely be required to maintain sufficient levels of genetic diversity (Weeks et al., 2011). Where multiple source populations are available, genetic diversity can be increased by mixing genotypes. This increases adaptive potential and enhances the likelihood of translocated populations becoming established (Sgrò, Lowe, & Hoffmann, 2011; Weeks et al., 2011), although consideration for outbreeding depression and transfer of maladaptive loci are required (Frankham, 2015).

Endangered or critically endangered species at immediate risk of extinction are often already suffering from a genetic viewpoint (inbreeding depression, loss of genetic diversity due to bottlenecks and drift, maladaptation, etc.). The initial levels of genetic diversity present in the source population(s), the number of individuals removed relative to the source population size and the population dynamics of the species will determine the magnitude of the impact on the source (e.g. Dimond & Armstrong, 2007). Accordingly, when translocating individuals, there is a trade-off between improving the survival rate and levels of genetic diversity of new populations and minimizing negative impacts on survival rate and genetic diversity of source populations.

1.3 | Case study

Effective monitoring is often lacking in translocations, yet is critical to understanding success and failure (Armstrong & Seddon, 2008; George et al., 2009; IUCN & SSC, 2013). Here, we look at a relatively rare example where the source populations of a species have been monitored prior to and following the removal of founder individuals to initiate replicate reintroductions. Our case study focuses on one of the Australia's smallest and most endangered fish: the redfin blue eye *Scaturiginichthys vermeilipinnis*, family Pseudomugilidae (Kerecsy, Kern, & Wager, 2019). Predation and competition with introduced eastern mosquitofish *Gambusia holbrooki* have likely led to the species' extirpation from all but a single spring (Kerecsy & Fensham, 2013). Human-mediated reintroductions have been implemented for redfin blue eye into several nearby invader-free springs. We provide a framework to determine the overall benefit (or risk) of translocations in redfin blue eye. We first estimate the overall survival probability of the species following translocations, accounting for the likelihood of translocation success and a decline in survival probability of the source population. We then determine the genetic diversity in each individual population, testing the hypotheses that: (a) genetic diversity will be reduced in translocated populations compared to the source due to failure to capture and retain genetic diversity and (b) genetic diversity of the source population will decline following the removal of founders. Finally, we determine the overall

genetic diversity of the species (in both the source and translocated populations) following translocation. For translocations to benefit redfin blue eye, the overall survival of the species should increase and the overall genetic diversity of a species should not be negatively impacted.

2 | MATERIALS AND METHODS

2.1 | Study species and study system

Redfin blue eye were discovered in 1990 (Ivantsoff, Unmack, Saeed, & Crowley, 1991) and are restricted to a small spring complex called Edgbaston in Queensland, Australia, which encompasses around 100 spring vents (see Supporting Information). Twenty-five endemic species have been recorded within the springs including two fish, 13 invertebrates and 10 plants (Rossini, Fensham, Stewart-Koster, Gotch, & Kennard, 2018). Many of the individual springs are very small and extremely shallow, rarely exceeding 5–10 cm in depth (see Supporting Information; Rossini, Fensham, & Walter, 2017). Individual springs are typically isolated by intervening desert, although major rainfall events potentially connect springs sporadically and may facilitate migration and genetic mixing of the biota.

Redfin blue eye are small (maximum wild length c. 30 mm) with a short life span (c. 12–18 months), fast reproductive cycle (females can breed continuously from 4 months of age laying 1–3 eggs per day over a 4- to 6-week period) and generation time of approximately 6–12 months (Fairfax et al., 2007; Wager & Unmack, 2000). The main threat to redfin blue eye is eastern mosquitofish, which appear to predate on and out-compete many native fish (Ivantsoff & Aarn, 1999; Kerecsy & Fensham, 2013). Localized extinctions are common following the establishment of the invader within a spring: since its discovery, the species has been extirpated from all but a single spring (NW30), with eastern mosquitofish invasion the likely cause in each case (Kerecsy & Fensham, 2013). The surface area of this spring is of average size for Edgbaston but is very shallow and has a census size ranging from approximately 300 individuals in autumn to approximately 1,000 individuals in spring (Fairfax et al., 2007). Conservation efforts have focused on protective fencing to exclude incursion of the invader into the single remnant population (Kerecsy, 2015), but also have the undesirable consequence of restricting natural re-establishment of the native species. Having the entire native species confined to only a single population constitutes a substantial extinction risk.

2.2 | Translocations

Human-mediated conservation reintroductions have been implemented for redfin blue eye into invader-free pools. The sole remaining population of redfin blue eye was used to source individuals (15–20 founders on each occasion) to initiate eight translocations between 2009 and 2012, with one of the more

successful translocated populations (T1) used to initiate an additional three populations (Figure 1). Barriers have been installed around springs with translocated redbfin blue eye to prevent the establishment of eastern mosquitofish and there are ongoing efforts to eradicate eastern mosquitofish from other springs (Kerezszy & Fensham, 2013). Monitoring surveys are conducted several times per year to ascertain the persistence of redbfin blue eye in the springs (see Supporting Information).

2.3 | Species survival

In the absence of actual survival estimates, we established a simple framework to study the effect of the translocation on the survival of the species. We assume that a translocation reduces the survival of the source population through the removal of individuals. This effect increases as the number of translocations increases.

$$S_{a,T} = 1 - (S_{n,T} - S_{1T} \cdot N).$$

The probability of survival after the translocation ($S_{a,T}$) equates to the probability of survival if no translocation had occurred ($S_{n,T}$) minus the effect of the translocation (S_{1T}) times the number of the new translocation (N) [assuming a linear effect of the effect of N].

For translocations to have a positive effect, the cost of a translocation in terms of the reduced probability of survival of the source population needs to be outweighed by the benefit, which is the

increase in the species' overall survival probability due to the newly established translocated populations. The combined probability of translocated populations establishing (E_{TT}) can be calculated via the formula below, where E_{1T} is the probability of a single translocation to establish successfully.

$$E_{TT} = 1 - (1 - E_{1T})^N.$$

So the combined survival probability of the translocation is the product of those terms:

$$T = S_{a,T} \cdot E_{TT}.$$

If T is larger than $S_{n,T}$ then the translocation will provide a benefit to the species' overall survival. For the framework we assume a broad but realistic range for all parameters [$S_{n,T} = (0.9, 0.1)$, $S_T = (0.001, 0.01, 0.1, 0.2)$, $E_{1T} = (0.1, 0.2, 0.3, 0.4, 0.5)$ and $N = (1..11)$] and calculate their effect (Figure 2). We then estimate the parameters for redbfin blue eye based on survey data and expert opinion.

2.4 | DNA collection, extraction and genotyping

Samples were collected from six populations of redbfin blue eye in 1990, 2010 and 2014 (including the source population, four translocated populations and one now extinct population, see Figure 1 for details). Fish were randomly sampled from across the available habitat in each individual spring. DNA from samples collected

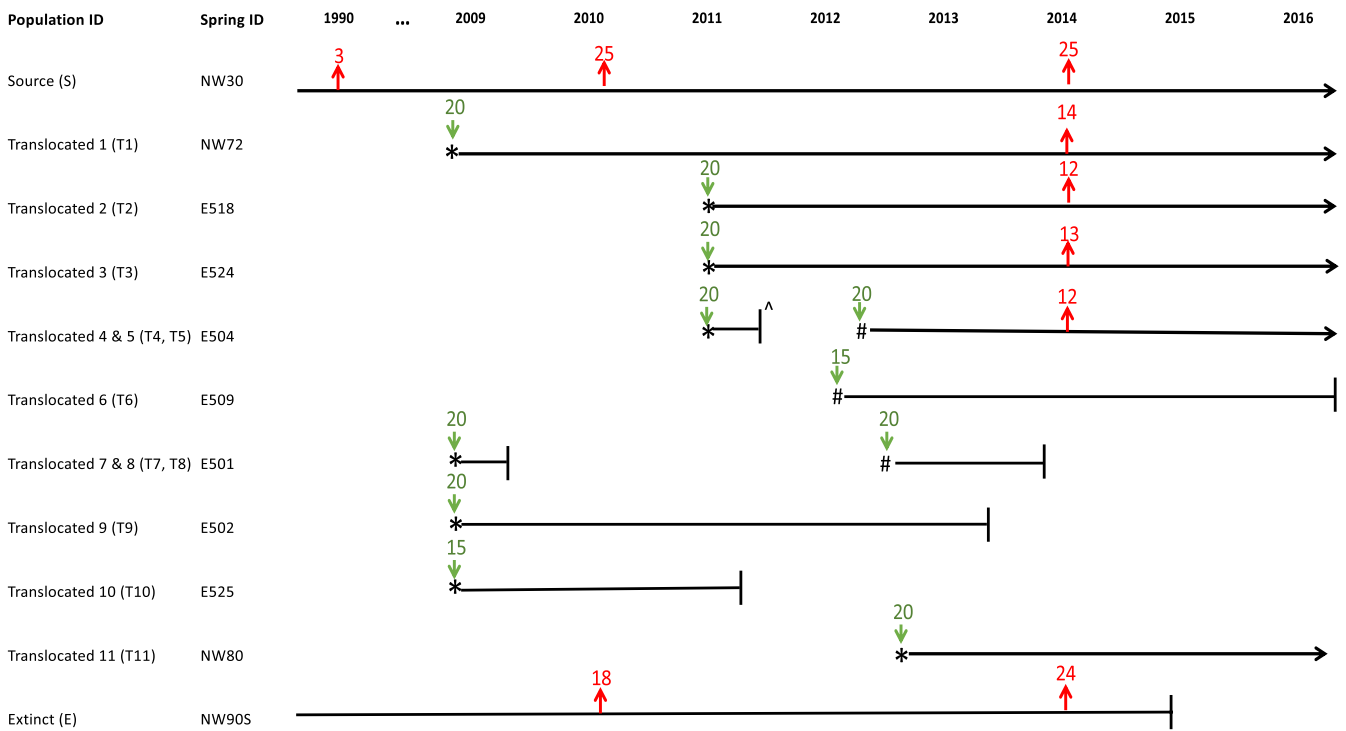


FIGURE 1 Redfin blue eye *Scaturiginichthys vermeilipinnis* distribution and persistence at the source, translocated and extinct remnant springs between 1990 and 2016 indicated by continuous black lines. Collection of genetic material (and number of samples) is indicated in red. Translocations initiated by founders from the source or T1 are indicated by asterisks or hashes respectively (and number of founders in green). ^Individuals returned to the source following detection of mosquitofish in spring

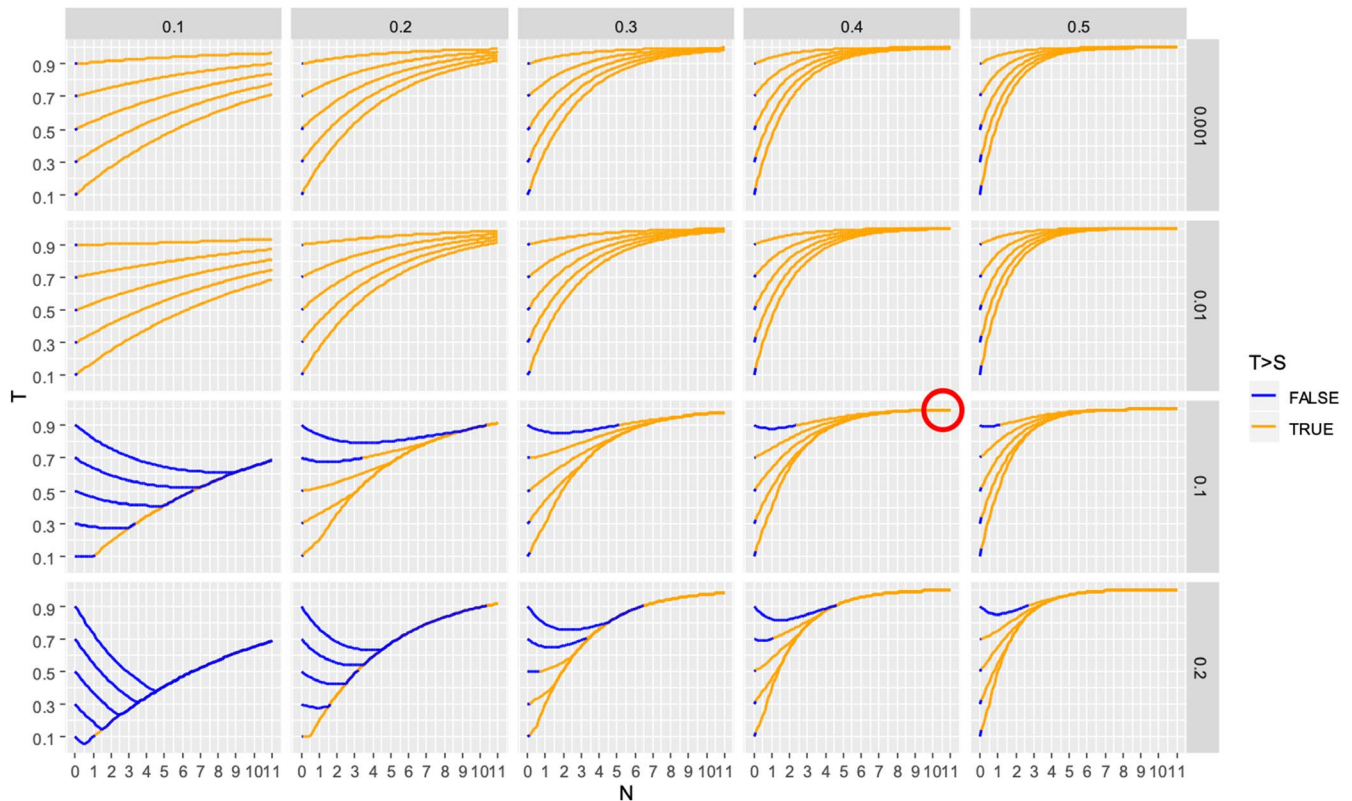


FIGURE 2 The predicted survival of a species after a given number of translocations. The bottom axis shows the number of translocations. The left axis indicates the overall survival of the species. The top axis indicates the likelihood of translocation success and the right axis shows the decreased survival of the species with each translocation. The yellow lines indicate where translocation has had a positive effect on survival. The red circle provides a conservative prediction on the short-term survival rate of redfin blue eye *Scaturiginichthys vermeilipinnis* following translocations

in 1990 and 2010 were extracted using a salting out method (Sunnucks & Hales, 1996) while 2014 samples were extracted by Diversity Arrays Technologies (DArT Pty Ltd) as per Georges et al. (2018). Genome-wide data in the form of SNPs (single nucleotide polymorphisms) were generated for all samples by DArT Pty Ltd using the DArTseq™ method (see Supporting Information). This resulted in 5,181 high-quality SNPs, which formed the basis of the analyses.

2.5 | Genetic analyses and simulations

Summary statistics (expected H_e and observed H_o heterozygosity, allelic richness A_R), fixation indices (F_{IS} and F_{ST}) and a principle coordinate analysis (PCoA) were performed on the data using the DArTR package (Gruber, Unmack, Berry, & Georges, 2018). A one-sided Wilcoxon signed-rank test was performed to determine the significance between source and translocated populations for expected and observed heterozygosity and allelic richness (Wilcoxon, 1945). Effective population size (N_e) was based on estimators from the R package NB (Hui & Burt, 2015), which estimates the effective population size based on two (or more) samples over time and was calculated for the source population. Generation lengths were set between 6 months and 1 year.

Pairwise relatedness was estimated between individuals using COANCESTRY 1.0.1.9 (Wang, 2011) to assess the level of relatedness in translocated populations compared with the source population. Pairwise relatedness was estimated based on the combined allele frequency of the source population from the three temporal samples using only SNPs that were polymorphic in the samples from the source population, totalling 5,121 SNPs. 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 the relative relatedness of populations across estimators would mean relative relatedness is robust to the estimator being used, which can occur regardless of differences in accuracy and precision among estimators (Attard, Beheregaray, & Möller, 2018; Attard, Brauer, et al., 2018).

We repeatedly simulated allele frequencies from a source population (1,000 times) in R using the DArTR package (Gruber et al., 2018; R Core Team, 2014). In each repeat we determined the number of alleles retained for a varying number of individuals sampled ($N = 1-80$) from the source population. For the simulation of allele frequencies of the source population we used the frequency of all

alleles present in the redfin blue eye source population sampled in both 2010 and 2014 (i.e. we assume that any 'new' alleles detected in 2014 were also present in 2010, but not sampled). We then compared the simulated number of alleles to the actual number of alleles retained within each translocated population and within the source population for each sampling regime.

3 | RESULTS

3.1 | Survival

In August 2016, redfin blue eye was found to persist in the source population (S) and in five of the 11 attempted translocations (see Figure 1). Population size estimates varied between the sites ranging from complete extirpation at several translocated populations to >1,000 individuals at T1 (see Supporting Information). Population size estimates for the source population appeared consistent with estimates obtained prior to the removal of founders, that is approximately 300 individuals (see Supporting Information).

Translocation success in the short term (i.e. self-sustaining population established and maintained over four to eight generations) occurred in five of the 11 translocation attempts ($E_{1T} = 0.45$). The cost of each translocation to the source is expected to be at least the impact of removing 15 founder individuals in autumn when the census population is approximately 300 individuals (Fairfax et al., 2007; i.e. $15/300$; $S_{1T} \geq 0.05$). The survival rate for redfin blue eye in the source population prior to translocations is likely to be greater than the success rate for translocated populations and less than one ($0.45 < S_{n,T} < 1.0$). Under these scenarios, the translocations are likely to have increased the species survival (in the short term) to almost one (Figure 2).

3.2 | Genetic diversity

In total, 146 redfin blue eye individuals were sampled between 1990 and 2014 and genotyped at 5,181 SNP markers. Levels of observed and expected heterozygosity were slightly lower in all translocated populations compared to the source (Table 1), although not significantly so (Table S1). Levels of allelic richness were significantly lower in all translocated populations compared to the source ($p < .001$, Table 1; Table S1). The now extinct remnant population (E) recorded the lowest levels of allelic richness, as well as observed and expected heterozygosity (Table 1). Significant levels of genetic differentiation were detected between the extinct population (E) and all extant populations (F_{ST} 0.236–0.398; Table S2). The translocated population T2 also showed significantly high levels of genetic differentiation from all extant populations (F_{ST} 0.079–0.104).

Based on a generation length of 6–12 months, approximately 4–8 generations have passed between the 2010 and 2014 genetic

TABLE 1 Genetic diversity of redfin blue eye for the source, translocated and extinct remnant populations estimated based on 5,181 SNP markers

Population (sampling date)	<i>n</i>	<i>A_R</i>	<i>H_o</i>	<i>H_e</i>	<i>F_{IS}</i>
Source (all)	53	1.95	0.284	0.286	0.015 (SD 0.012)
Source (1990)	3	N/A	N/A	N/A	N/A
Source (2010)	25	1.95	0.289	0.284	0.002 (SD 0.217)
Source (2014)	25	1.94	0.278	0.281	0.016 (SD 0.224)
Translocated (all)	51	1.77	0.267	0.276	−0.019 (SD 0.013)
Translocated 1	14	1.82	0.275	0.266	−0.016 (SD 0.271)
Translocated 2	12	1.76	0.245	0.236	−0.049 (SD 0.256)
Translocated 3	13	1.69	0.284	0.264	−0.058 (SD 0.255)
Translocated 5	12	1.77	0.263	0.248	−0.050 (SD 0.269)
Extinct (all)	42	1.71	0.187	0.184	−0.018 (SD 0.021)
Extinct (2010)	18	1.58	0.223	0.196	−0.108 (SD 0.212)
Extinct (2014)	24	1.47	0.162	0.154	−0.023 (SD 0.249)

Abbreviations: *A_R*, allelic richness; *F_{IS}*, inbreeding coefficient; *H_e*, expected heterozygosity; *H_o*, observed heterozygosity; *n*, number of individuals genotyped for each population.

sampling of the source population. The effective population size of the source in 2014 is estimated to be between 177 and 354 individuals (Table S3). If we assume six generations have passed between sampling periods, the effective population size of the source in 2014 is estimated to be 266 individuals (CI 223.8–324.4).

The average pairwise relatedness in the source population was similar across temporal samples, and this was regardless of the relatedness estimator used (Figure S1). All translocated populations showed increased relatedness compared with the source population, and translocated populations that had greater genetic divergence from the source also had a greater level of relatedness (Figure S1). *F_{IS}* values among the populations were similar and statistically non-significant ($p > .05$; Table 1).

Low to high genetic differentiation was detected between the extinct population, the source population and the translocated populations (F_{ST} 0.004–0.398; Table S2; $p < .001$). The extinct population (2010 and 2014) showed the greatest level of divergence from all other populations, while the source (2010 and 2014) and T1 populations showed the lowest level of differentiation.

Results from the PCoA corroborate the genetic differentiation detected by F_{ST} , with clear cluster separation among all populations and greatest separation between the extinct (2010 and 2014) populations and all other populations (Figure S2). PCoA (Figure 3) shows little evidence of genetic differentiation in the source population across the two sampling periods (i.e. 2010 and 2014), although F_{ST}

FIGURE 3 Principle coordinates analysis indicating the genetic relationship among redfin blue eyes *Scaturiginichthys vermeilipinnis*. Each dot represents an individual, color-coded according to the population of origin. The plot is based on an analysis of 5,181 single nucleotide polymorphism loci

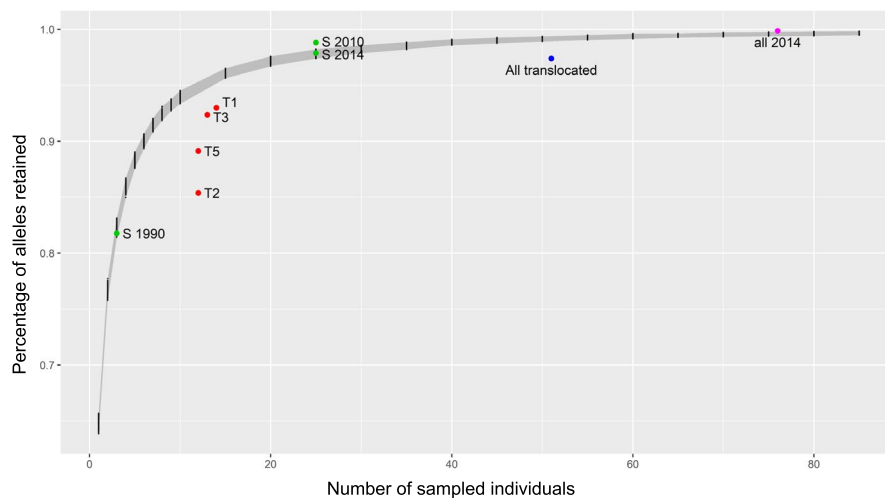
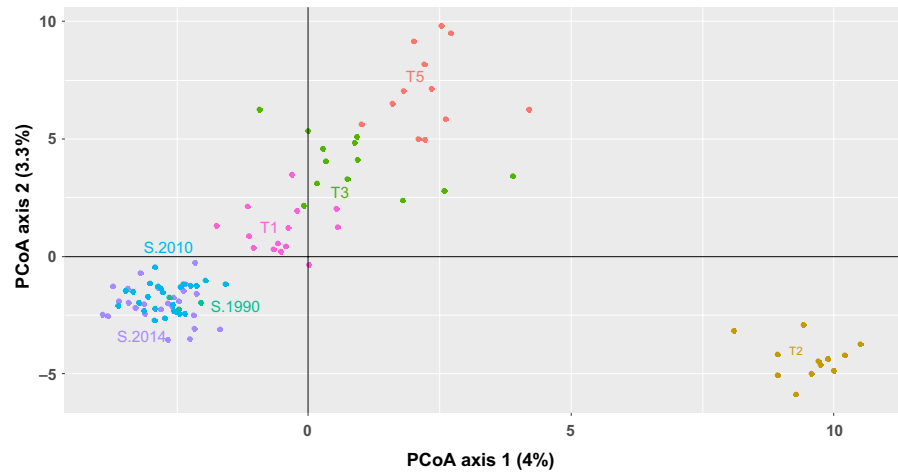


FIGURE 4 The percentage of redfin blue eye *Scaturiginichthys vermeilipinnis* alleles retained for a given number of individuals sampled from a population. The vertical black lines and grey confidence envelope show the expected percentage of alleles retained (95% CI) based on simulations of allele frequencies from the source population (S). The green and red dots indicate the actual percentage of alleles retained within the source population (sampled in 1990, 2010 and 2014) and four translocated populations (T1–T3 and T5) respectively. The blue dot indicates the total percentage of alleles actually retained in all translocated populations combined while the pink dot indicates the total percentage of alleles retained in all populations persisting in 2014

analyses reveal a low, but significant level of genetic divergence (F_{ST} 0.004; $p < .001$; Table S2). Genetic data obtained from four translocated populations after several generations in isolation reveal they have genetically diverged from each other and the source (Figure 3). The translocated population T2 is the most genetically dissimilar from all other extant populations analysed.

The empirically estimated proportion of alleles retained within the source population across the three sampling time periods remained consistent with expectations based on simulations (Figure 4). Initiating translocated populations T1, T2, T3 and T5 with 20 founder individuals is expected to capture approximately 97.5% of the genetic diversity of the source population (although note that T5 was founded by T1 individuals). After 3–6 years of breeding, however, the proportion of alleles retained has diminished in each of the translocated populations, suggesting unrepresentative capture of alleles or uneven breeding contribution from

the founders. Collectively, the translocated populations retained approximately 97.5% of redfin blue eye alleles suggesting that a different suite of alleles had been retained within each population. Genetic diversity was well-maintained for the species overall when all populations sampled in 2014 (i.e. translocated and source) are considered.

4 | DISCUSSION

Conservation translocations provide an opportunity to establish new populations, potentially increasing the overall survival of a species. Translocations come with benefits and risks to the population demography and population genetics of a species, and these can act in opposing ways. Replicate translocations undertaken for the critically endangered redfin blue eye allowed us to investigate both

the genetic and demographic impacts on source and translocated populations using simulations and genetic analyses. The theoretical approach developed here can be applied to other systems to assess the benefits and risks of translocations.

Redfin blue eye represent a species on the brink of extinction, having declined to a single remnant population. Since 2009, redfin blue eye populations reintroduced to invader-free springs resulted in successful establishment approximately 45% of the time, reaching carrying capacity within a few years and increasing the species' overall census size. Our simulations revealed that, provided the initial survival of the remnant population was <1 , the translocations are likely to have had a positive effect on the short-term survival of redfin blue eye. In general, a positive effect of translocation is expected if the number of newly initiated populations is large (>10) and the probability of translocation success is not too low (>0.2). With the risk of extinction due to stochastic events now spread across several populations, the overall survival probability of the species has increased, at least in the short term.

Genetic analyses support our first hypothesis that translocations result in reduced genetic diversity in each translocated population due to failure to capture and retain genetic diversity. Each translocated population of redfin blue eye had managed to retain only a subset of the genetic diversity of the source population, had significantly reduced allelic richness and had increased relatedness. The effective population sizes of the translocated populations are likely to be insufficient to avoid fitness loss from genetic drift and inbreeding, even in the short term (i.e. $N_E < 100$; Frankham et al., 2014; Lande, 1998). Although it is likely that too few generations have passed for inbreeding to be apparent (F_{IS} values are non-significant), without intervention these translocated populations will likely experience increased inbreeding over time (Frankham et al., 2014). Genetic dissimilarity is already apparent among the source population and each of the four translocated populations (Figure 3), with the large genetic differentiation apparent in T2 likely due to an initial reduction in population size and delayed population expansion (see Supporting Information).

Our second hypothesis was also supported: that genetic diversity of the source population will decline following the removal of founders. Allelic richness and observed and expected heterozygosity declined in the redfin blue eye source population following founder removal (Table 1) and genetic diversity of the source population differed significantly between 2010 and 2014 ($F_{ST} 0.004$, $p < .001$). Although we cannot rule out random sampling effects or genetic effects such as drift contributing to the loss of genetic diversity in the source population, the source's estimated effective population size of approximately 260 individuals is likely to be sufficient to prevent inbreeding depression and limit fitness loss in the short term but inadequate to retain adaptive potential in the long term (Frankham et al., 2014; Lande, 1995; Willi, Van Buskirk, & Hoffmann, 2006). Conserving this remnant population in isolation, therefore, does not provide a viable long-term option. The extinct remnant population was genetically differentiated from all extant populations (Table S2; Figure 3), although it had low levels of diversity (Table 1). The failure to source founder

individuals from this population prior to its extinction in 2015 means that, as a species, redfin blue eye have lost a substantial amount of nuclear and mitochondrial diversity (Faulks, Kerecsy, Unmack, Johnson, & Hughes, 2017). Ensuring all extant populations are represented in translocated populations provides the best opportunity to maintain high levels of genetic diversity in newly established populations.

Drift is likely to slowly erode genetic diversity in redfin blue eye unless the global effective population size can be increased to maintain diversity (Allendorf & Ryman, 2002). Establishing new populations via translocation, as was done between 2009 and 2012, provided a means to achieve an increase in global effective population size. Although each translocated population retained only a subset of the genetic diversity of the source, the four translocated populations combined retained approximately 97.5% of the species' extant genetic diversity (Figure 4). This is likely due to the capture and retention of different alleles. The small habitat size and artificial isolation of these populations (due to mosquitofish exclusion fences), however, restrict population growth and effective population size, which will lead to further erosion of genetic diversity over time. We therefore recommend maintaining a low level of ongoing human-mediated gene flow to maintain fitness among these small, isolated populations and to retain adaptive potential within the species (e.g. one migrant per generation; Mills & Allendorf, 1996). Repeated translocation events such as this have been shown to maintain or increase genetic diversity and fitness for populations of mammals, birds and reptiles (Heber et al., 2013; Michaelides, Cole, & Funk, 2015; Weeks et al., 2017).

Where possible, we also recommend wild-to-wild releases as conducted here, rather than captive-to-wild release. This is because captive breeding is not suitable for many species (redfin blue eye have proven difficult to breed in captivity with declining recruitment over a 3- to 5-year period; Tappin, 1999), can cause detrimental behavioural and disease effects (Frankham, 2008; Snyder et al., 1996) and is likely to be cost- and time-intensive to initiate and maintain. Wild-to-wild releases also generally show greater rates of success (Christie, Marine, French, & Blouin, 2012; Snyder et al., 1996). If there is sufficient time before demographic collapse (Woodruff, 1990), improvements in the wild-to-wild release could include genetic assessment of wild individuals (or populations) prior to translocation to identify the optimal strategy for selection of founder individuals (Miller et al., 2017; Sandoval-Castillo et al., 2017). If the source population is not robust enough to support wild-to-wild translocation, captive breeding may be required. If so, captive breeding should be conducted in as few generations as possible and in a way that minimizes inbreeding and the loss of genetic diversity (Attard et al., 2016; Witzemberger & Hochkirch, 2011). Conservation management decisions will therefore differ according to current demographic and genetic factors as well as species life history, such as generation length and mating system (Robert et al., 2007). The benefits and risks of these alternative approaches need to be evaluated to ensure the strategies selected provide the best opportunity to improve conservation outcomes for the species.

5 | CONCLUSIONS

As threatening processes continue to reduce population sizes and drive species closer to extinction (Ceballos et al., 2015; IUCN, 2009; Urban, 2015), the stakes become higher with regard to the potential benefits and risks of translocations. We have shown that translocations can result in reduced genetic diversity in newly established populations, as well as the source population, compared to the source population prior to the removal of individuals. Despite this, the species may still retain a high level of genetic diversity overall if translocated populations retain a different subset of alleles. In addition, the overall impact of translocations on species survival may still be positive, at least in the short term, provided source populations are capable of sustaining the loss of individuals and potential loss of genetic diversity (IUCN & SSC, 2013). We recommend applying this framework to other species to weigh up translocation trade-offs on a case-by-case basis to identify the optimal management solution.

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AUTHORS' CONTRIBUTIONS

E.M.F., B.G. and P.J.U. conceived the ideas and designed the study; L.K.F., A.K. and P.J.U. conducted fieldwork; B.G., C.R.M.A. and P.J.U. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.rv15dv44x> (Furlan et al., 2020).

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SUPPORTING INFORMATION

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