Conservation Genetics (2023) 24:869–882
https://doi.org/10.1007/s10592-023-01541-2

RESEARCH ARTICLE

# Optimizing targeted gene flow to maximize local genetic diversity: when and how to act under various scenarios of environmental change

**Adam S. Smart**[1] · **Ben L. Phillips**[1]

Received: 27 April 2022 / Accepted: 9 June 2023 / Published online: 4 July 2023


**Abstract**
Targeted gene flow is an emerging conservation approach which involves introducing a cohort of individuals with particular traits to locations where they can produce a conservation benefit. This technique is being proposed to adapt recipient populations to a known threat, but questions remain surrounding how best to maximize conservation outcomes during periods of continuous directional environmental change. Here we introduce a new management objective—to keep the recipient population extant and with maximum diversity of local alleles—and we explore how varying the timing and size of an introduction can maximise this objective. Our results reveal a trade-off between keeping a population extant and maintaining a high level of genetic diversity, but management levers can often optimize this so that nearly 100% of the allelic diversity is preserved. These optimum outcomes sets are highly sensitive to the predicted rate of environmental shift, as well as the level of outbreeding depression in the system.

**Keywords** Assisted gene flow · Conservation genetics · Individual based modelling · Evolutionary rescue · Population modelling · Management objective · Population viability analysis

## Introduction

Widespread and rapid environmental change is forcing many species to drastically alter how they interact with and respond to the environment (Hoffman and Sgro 2011). As these changes become harder to mitigate and manage, imperilled populations may survive by shifting their geographic range, through phenotypic plasticity, or via genetic adaptation (Nunney 2016). However, it is increasingly difficult for populations to shift their range because many plant and animal species exist in fragmented habitat and do not possess the dispersal ability to navigate between suitable patches (Tingley et al. 2009; Ralls et al. 2018). It is also unclear how often plasticity will provide a long-term advantage since plasticity may or may not be aligned in an adaptive direction, and may also reduce the effectiveness of natural selection in driving adaptation to changing conditions (Ghalambor et al. 2007; Chevin and Hoffman 2017; Noble et al. 2019). Genetic adaptation is the most robust solution to directional environmental change, and for populations with suitable standing genetic variation, rapid adaptation may forestall extinction through evolutionary rescue (Cook and Sgro 2017; Bell et al. 2019; Harris et al. 2019). But for many species, necessary traits are either locally absent or at low frequencies, slowing the evolutionary response and priming populations for extinction (Lacy 1997; Hoffman et al. 2017; Pavlova et al. 2017).

One way to increase the chance of evolutionary rescue is to provide populations with the genetic variation necessary for adaptation (Frankham et al. 2002). Some strategies advocate simply increasing genetic variation, in a non-directional manner (Waller 2015). Such "genetic rescue" is particularly powerful when populations have low diversity and are suffering inbreeding depression (Lande and Shannon 1996; Hedrick and Fredrickson 2010). Other strategies take a more targeted approach seeking to increase genetic variation in the direction needed to adapt. This idea of introducing individuals with pre-adapted traits into a population was

✉ Adam S. Smart
asmart1@student.unimelb.edu.au

Ben L. Phillips
phillipsb@unimelb.edu.au

[1] School of BioSciences, University of Melbourne, Parkville, VIC 3010, Australia

first proposed as a possible response to the impact of climate change, where the idea was termed "assisted gene flow". It is, however, a strategy that can be applied to broad suite of conservation problems, and in recognition of this broader application we refer to it here as "targeted gene flow". Conservation managers have already begun to employ targeted gene flow (TGF) with the aim of increasing the frequency of pre-adapted traits in threatened populations (Aitken et al. 2013; Kelly and Phillips 2018, 2019; Weeks et al. 2017; Indigo et al. 2018). For example, Kelly and Phillips 2016 have identified behavioural responses in surviving population of Northern where individuals ignore cane toads as a food item (i.e. toad naïve traits), and that such responses have high heritability (> 30%) even if a single parent exhibits the toad native behaviour. Whilst work is underway to examine the utility of TGF, more work is required to define the associated risks and costs compared to other conservation actions.

Relative to other conservation actions, TGF will tend to be very cost effective, but it is not without risk: outbreeding depression (Frankham et al. 2011), genetic swamping, and disease transmission (Cunningham 1996; Sainsbury and Vaughan-Higgins 2012) are all possibilities to be considered. Because of risks and costs, any conservation action needs to be characterized to allow scenario-testing, cost-benefit analysis, and to provide managers with realistic expectations (Knight et al. 2006a; Weeks et al. 2011; Weeks et al. 2016; Burbridge et al. 2011); TGF is no different. While conservation managers regularly use population models to assess alternative scenarios, adaptive evolutionary processes are rarely included in models of population viability (Lacy 2019) or in cost-benefit exercises (Klein et al. 2009). By its nature, TGF requires models that incorporate evolution into population viability and cost- benefit analyses.

The stated aims of conservation translocation actions are usually to create or maintain viable populations of a single, focal species, by moving individuals from one area of the landscape to another suitable area to produce a conservation benefit. Such actions are can be conducted as a once off, or be staged through time, with measures of success based on abundance (establishment, fecundity and population size), extent (dispersal, number of populations), resilience (genetic variation, resistance to perturbation), persistence, or any combination of the above with respect to the recipient population (Pavlik 1996; Vallee et al. 2004; Commander et al. 2018). With TGF we want a viable population, but we want to avoid swamping the local genome in the process. Swamping the local genome with introduced alleles that have historically been absent, is akin to extinction and reintroduction, and one of the great promises of TGF is that we might both prevent extinction and conserve local genetic diversity in the process: the aim being to manipulate populations so that they are not only locally adapted but carry genes that allow them to survive under future environmental shifts (i.e. have high adaptive potential) (Harris et al. 2019). Given the complexity of prioritizing management actions across multiple measures of success, we need a clear statement of our management objective (Regan et al. 2005). Here we propose a robust objective: to keep the recipient population extant and to achieve this whilst maintaining the genetic diversity currently present. While extinction is straightforward, diversity is a rich concept that admits a wide range of possible definitions (see Morris et al. (2014) for a concise summary). We focus here on the maintenance of genetic diversity through maintaining, as far as possible, the set of alleles that are initially present in the recipient population, including the evenness at which these occur. This provides an objective that considers not only the richness of genetic material remaining but the evenness at which this material occurs. Aside from the total number of alleles present in a population the distribution of their abundances is also an important component of diversity. If an allele is represented in only a tiny percentage of individuals, it should be clear that it contributes less to the population's diversity than an allele represented in 50% of the population. The importance of allelic evenness has received less attention than that of richness but its value seems inarguable.

We equate our management objective to a gambler's return on investment: the probability of winning (avoiding extinction) multiplied by the payout (the remaining allelic diversity at the end of the management horizon). To achieve this, we incorporate our probability of 'winning' $(1 - x)$, where $x$ is the extinction probability, with a common measure of genetic diversity, the *Gini-Simpson Index*. The Gini-Simpson Index of diversity ($D$) is equivalent to the expected heterozygosity under Hardy-Weinberg equilibrium and is a common measure of diversity (Guiasu and Guiasu 2012; Morris et al. 2014), where 1 represents maximum diversity, and 0, no diversity. Thus our objective is to maximise the expected return:

$$\mathrm{E}(Y) = D \cdot (1 - x),$$

where we calculate $D$ using only alleles initially present in the recipient population. The problem we address is a general one: how does varying key management levers influence the expected return of a TGF action? Specifically, we are interested in exploring how adjusting two factors—the number of years before a potential threat arrives (i.e. the timing), and the size of the group introduced at this time (i.e. the size)—can impact the expected outcome of the TGF strategy. We explore this question across a range of scenarios of environmental change ranging from near step changes to a much more gradual environmental shift. We explore the influence of a continuous gradual shift in the environment, similar to climate change projections (IPCC ARC6 Climate

Change 2021), as well as threats that constitute a shorter, more drastic change in environmental suitability, such as the introduction of a wildlife disease or the invasion of a pest species.

We utilize a discrete-time individual-based population model with the goal of exploring the optimal timing and size of a TGF action across various scenarios of environmental change. Our model is structured such that it is flexible across study species and various projections of environmental change. Against our new management objective, we explore the sensitivity of the optimal choice of management strategy across a wide range of demographic, evolutionary and environmental parameter values.

## Materials and methods

Individuals in the model have a maximum rate of reproduction, $R_{\max}$, modified by density dependence (described using the Beverton–Holt model of population growth (Beverton and Holt 1957) and a fitness multiplier (see below) which yields an individual's expected reproductive output:

$$E(W_i) = \frac{R_{\max} \cdot w(z_i, t)}{1 + \left(\frac{R_{\max}-1}{N^*}\right)N_t}. \quad (1)$$

Here $N_t$ represents the number of individuals present in the population at time $t$. $N^*$ denotes the carrying capacity that would be achieved if all individuals reached a fecundity of $R_{\max}$. The fitness multiplier $w$ references an individual's phenotype ($z_i$) in relation to the environmental optimum at time, $t$. In our reference case we set $R_{\max} = 2$ and $N^* = 1000$, but explore a sensitivity analysis on $R_{\max}$ and $N^*$ to determine the impact of demographic parameters on our result (see Scenarios). Each individual is treated as a sexual hermaphrodite and has a chance to breed with a randomly selected mate.

### Sexual reproduction

Each individual's genotype consists of a number of diploid, biallelic loci. A subset of these loci, $n_p$ contributes to an individual's phenotype; $n_c$ are involved in incompatibility; $n_n$ are neutral and used to track the recipient genome; and $n_h$ are used to score the heterozygosity of each locus through time. We differentiate between loci used to track the recipient genome and those used to track heterozygosity in order to compare two contrasting management objectives (see below). Each offspring's genotype is a result of the fusion of gametes from a 'male' and 'female' parent. Genetic recombination is based on an algorithm described by Kelly et al. (2018) in which the genome wide recombination rate is calculated as the average proportion of pairwise crossover events between loci.

### Evolutionary dynamics

Each individual expresses a continuous trait, $z$ determining how well adapted the individual is to the environment in a given timestep. The trait $z$ experiences stabilising selection against an environmental optimum that shifts over time (see below). This trait value is determined according to the underlying mechanics of a simple quantitative genetic model, such that the phenotypic variance ($V_T$) is the sum of genetic and environmental contributions: $V_T = V_G + V_E$. Within all our simulations the total variation of the trait remains constant ($V_T = 1$).

### The genotype and expected trait value

Each locus with phenotypic effects (within $n_p$) has an equal and additive effect on the individuals expected trait value, E($z$). Two alleles are possible at each locus, with alleles having a value of either 0 or $d$, where $d > 0$. This additive effect size $d$ is calculated as a function of the environmental variance ($V_E$), the trait heritability ($h^2$), and is chosen such that the stated heritability is achieved at initialisation (given $V_E$, $n_p$, and the initial frequency of alleles with effect size $d$, $f_0$):

$$h^2 = \frac{V_G}{V_G + V_E},$$

or, equivalently,

$$V_G = \frac{h^2 V_E}{1 - h^2},$$

With a binomial distribution, the expected genetic variance is then given as,

$$V_G = 2d^2 n_p f_0 (1 - f_0),$$

where $f_0$ is the initial frequency of favourable alleles present (i.e. those with effect sizes of $d$) at the start of the simulation. We vary this value of $f_0$ in our sensitivity analysis. Our effect size, $d$ can be calculated as:

$$d = \sqrt{\frac{h^2 V_E}{2n_p f_0 (1 - h^2)(1 - f_0)}}.$$

Each individual's expected phenotype is given by:

$$E(z_i) = d \sum_{j=i}^{n_p} \sum_{k=1}^{2} a_{i,j,k},$$

where $a_{j,k}$ references the allelic value $k$ (either 0 or 1) of locus $j$. Here the individual is represented by $i$. In our

reference case we set heritability of the trait in the recipient population ($h^2$) to 0.1. We explore the impact of differing heritability values in the sensitivity analysis. We centre the mean phenotype such that maximum fitness is conferred at the start of the simulation.

## The phenotype

An individual's realised phenotypic value, $Z_i$, incorporates environmental variation on the expected trait value, and is determined stochastically, as a draw from a normal distribution.

$$z_i \sim N(E(z_i), V_{\mathrm{E}}). \tag{2}$$

## The changing environment

We model a shift in the suitability of the recipient's environment across our management horizon at each timestep, $v_t$, via a sigmoidal curve defined by the equation:

$$v_t = \frac{c}{1 + e^{\text{-m}(M - \frac{M}{2})}}, \tag{3}$$

where the upper asymptote, $c$, is the distance from the initial trait mean at $t=0$ measured in standard deviations of the initial phenotype distribution (set to 2 within all simulations). The rate at which the environmental optimum shifts each generation is defined by a 'flattening constant', $m$. An individual's realised phenotypic value ($z_i$) is referenced against this optimum value, $v_t$, at each timestep to calculate the individual's fitness as a function of time.

## The environment and fitness

Individual fitness ($w_i$) changes according to the distance between an individual's trait value ($z_i$) and the environmental optimum ($v_t$) according to,

$$w_{i,t} = e^{-k(z_i - v_t)^2}. \tag{4}$$

We can then relate the change in fitness ($w$) over management time ($t$), via substituting (3) into (4) and solving for the differential with respect to $t$:

$$\frac{dw}{dt} = \frac{c \cdot e^{2(km)}}{(1 - e^{m(t-25)})^2}.$$

Given (3), the maximum rate of environmental change occurs at $v_{25} = c/2$, setting $t=25$ and $z$ at its initial mean value ($z=0$), we can solve for the maximum demographic pressure exerted on our population:

$$\left.\frac{dw}{dt}\right|_{\substack{t=25 \\ z=0}} = \frac{-kce^{-mt-k^2}}{4}.$$

It is clear that this maximum pressure can be modified by changing either the absolute magnitude of shift ($c$) or the flattening constant, $m$. Thus by changing either $c$ or $m$ we can explore varying demographic pressures; we have chosen to explore a range of $m$ in what follows.

## Loci involved with incompatibility

To allow the model to explore outbreeding depression, each individual carries $n_c$ loci involved with genetic incompatibility. These loci carry fixed difference between recipient (a = 0) and source (a = 1) populations. These loci are used to implement outbreeding depression using a model of two-locus incompatibilities developed by Turelli and Orr (2000). The Turelli and Orr model implements the idea that lowered hybrid fitness can be explained by between-locus Dobzhansky-Muller incompatibilities and considers three types of incompatibility: those between heterozygous loci ($H_0$), those between a heterozygous and a homozygous locus ($H_1$), and those between homozygous loci ($H_2$). Their model describes a 'hybrid breakdown score' (E($S$) of an individual based on the frequency of each type of incompatibility in the individual's genome. These are calculated from the proportion of loci that are homozygous from the recipient ($p_1$) and source populations ($p_2$), in addition to the proportion that are heterozygous for material from the two populations, $p_{\mathrm{H}}$. We use our set of $n_{\mathrm{c}}$ incompatibility loci to calculate these values of $p$ for each individual. Following Turelli and Orr, the hybrid breakdown score is given as,

$$E(S_i) = n_c[p_1 p_2 H^2 + (p_1 + p_2) p_H H_1 + p_H^2 H_0].$$

A negative exponential link is used to relate the hybrid breakdown scores to fitness,

$$s_i = e^{-\alpha E(S)},$$

where $\alpha$ is a constant, and $s_i$ is the probability of survival from outbreeding depression. When outbreeding depression is activated in the model, all individuals' survival probabilities are multiplied by an individual's $s$ value (set to 1 otherwise), and survival is determined as a draw from a Bernoulli distribution with the resultant survival probability. A simple dosage ratio is used for the different classes of incompatibility to generate the hybrid breakdown score: $(H_1) = 0.5$,

$(H_2) = 1$ and $(H_0) = 0.25$. The value of $\alpha$ is varied to manipulate the strength of outbreeding depression in the model.

## Neutral loci

To track the proportion of the recipient population's genome remaining at the final timestep, each individual is initialised with $n_n$ neutral loci, which carry fixed differences between recipient (a = 0) and introduced (a = 1) populations. We calculate the proportion of loci which retain alleles from the recipient genome ($r_p$) at the end of a given simulation run and use this measure to compare management objectives.

## Allelic diversity of the recipient population

We track the allelic diversity of a population through time by initializing each individual with $n_h$ loci, which carry fixed differences between recipient (initialised with a = 0 or 1 with equal probability) and introduced (a = 2) individuals. We use this set of loci to generate a measure of allelic diversity taking into account the number of recipient alleles present (diversity) as well as the relative abundance of each allele (evenness). Because we assume all alleles have an equal and additive effect on an individual's trait value (i.e. no disparity) we use the Gini-Simpson diversity index ($D$) as our measure of diversity, defined as:

$$1 - D = \sum_{i=1}^{j} \left( \frac{n_j(n_j - 1)}{(N \cdot 2n_h)(N \cdot 2n_h - 1)} \right),$$

where $n_i$ is the number of alleles from the recipient population (a != 2) across all individuals at locus j, $N$ is the population size and $2n_h$ is the total number of biallelic loci in the population. We subtract $D$ from 1 to give our final diversity measure (hereafter D for simplicity) a range from 0 (low diversity) to 1 (high diversity). As allelic richness and evenness increase, so diversity increases. We can then use this measure of allelic diversity in conjunction with extinction risk to optimise the timing and size of a TGF action.

## Targeted gene flow

To simulate a TGF action, we introduce a number of differently adapted individuals into the recipient population from a 'source' population. This source population is adapted to the future environment of the recipient location at the end of the management horizon. Given an input value for $c$ and $m$ can solve for the frequency of favourable alleles required to be optimally adapted at management time $M$ (see S4 for full workings).

$$\hat{f}_M = \frac{v_M^2}{2n_p V_G + v_M^2}.$$

We then explore a management space, varying the timing of an introduction and the number of introductees. In our test case we introduce individuals adapted to $t = 50$, i.e. a population adapted to the environment at our management horizon at $M = 50$ years. Across this space we explore introduction times from 0 to 50 years, at two-year intervals. The proportion of introduced individuals ranges from 0 to 0.3, in step increments of 0.025, for each introduction time. This proportion is in relation to the population size at the time of the management action, $N_t$, and not to the carrying capacity, $N^*$.

## Management scenarios

We define a 2-dimensional management space in which we examine the effect of varying the timing of introductions and the proportion of pre-adapted individuals introduced. At each part of management space we run 100 replicate simulations of the model and average results across these replicates. Each replicate begins with an adapted population of $N$ individuals - the 'recipient' population. The recipient population is initialised with an initial mean phenotype described by (2). The number of loci per individual is set to 80 ($n_p = 20$ relating to the trait, $n_c = 20$ relating to incompatibility, $n_n = 20$ neutral loci and $n_h = 20$ used to track allelic diversity). Carrying capacity of breeding individuals was set to 1000 in the test case. The recipient population is allowed to grow for 10 years before the environment starts to change. Over all simulation runs we record whether the population goes extinct or not by the management horizon, $M$. For surviving populations, we calculate the Gini-Simpson diversity index, $D$. We use these two measures (extinction, and allelic diversity) to calculate our management objective, E($Y$) the maximum expected diversity return - the proportion of allelic diversity likely to survive the change in environmental suitability.

## Sensitivity analysis

The above management space was repeated across combinations of parameter space to produce a global sensitivity analysis around key parameters (see Table 1 for a full list of input values and S3 for further detail). A full sensitively analysis of our our 7-dimensional parameter space in a fully factorial design to determine the impact of varying the initial frequency of favourable alleles ($f_0$), growth rate ($R_{max}$), heritability ($h^2$), the initial size of the population ($N$), the maximum selective pressure exerted on the population ($\delta$), the rate of genetic recombination $r$, and the strength of outbreeding depression ($\alpha$). For each parameter set, we explore the

**Table 1** Parameter inputs for generic individual-based model. Maximum demographic pressure refers to the highest change in environmental suitability across a timestep experienced by our simulated population (see S1 for more information).

| Parameter | Description | Input values |
|---|---|---|
| $f_0$ | Initial frequency of favourable alleles | 0.05, 0.3 |
| $h_2$ | Heritability of alleles | 0.1, 0.2, 0.3 |
| $R_{max}$ | Maximum reproductive rate | 2, 3, 5 |
| $N^*$ | Carrying capacity of simulated population | 500, 1000. 2000 |
| $\delta$ | Maximum demographic pressure | 0, 15, 0.3, 1 |
| $r$ | Rate of genetic recombination | 1.333, 50 |
| $\alpha$ | Strength of outbreeding depression | 0, 0.04, 0.28 |

full management space and record the maximum expected diversity return (E($Y$) as well as where in the management space this maximum is recorded. Model simulations were implemented in R (version 3.6.0; Team 2016) and C++, and run using Spartan, a High-Performance Computing System operated by the Research Platform Services at The University of Melbourne (Lafayette et al. 2016).

## Results

Across all simulations we found that the success of a given gene flow action was strongly influenced by the timing of the introduction as well as the proportion of pre-adapted individuals introduced at a given timestep (Figs. 1 and 2). The management objective (E($Y$)) was optimised when a greater proportion of individuals (10% or above) were introduced in the years prior (or during) the maximum level of demographic pressure experienced by our simulated populations (~25 years into the simulation). Although this pattern remained consistent throughout, adjusting the demographic parameters did alter the effectiveness of TGF, and the optimal management strategy (Figs. 3, 4 and 5).

Trait heritability ($h^2$) impacts the success of our simulated management actions. Higher heritabilities generally increased the expected return, with particular respect to scenarios where there is a lower carrying capacity (Fig. 2). These broad patterns were also seen in the sensitivity analysis suggesting they are consistent trends robust to population dynamics. A high carrying capacity in the system seemed to negate the influence of a reduced heritability and the effects of faster environmental decay (Fig. 2a). Across all scenarios, the optimal timing and size of an introduction favoured scenarios with a high number of individuals introduced in the years immediately prior to the greatest shift in the environment (Fig. 1c), which occurs halfway through the management horizon at year twenty-five.

The chosen shape of environmental shift changed the maximum expected return as well as the optimal location in management space (timing and size) (Fig. 6). Scenarios with a gradual environmental shift produced a higher expected return than scenarios with a severe (and rapid) level of environmental shift. In addition, increased levels of demographic pressure constrained the optimal time to implement TGF, often clustering around the years immediately preceding the maximum rate of change (Figs. 1c and 3a and b).

Outbreeding depression drastically reduced the success of targeted gene flow, in some cases generating no improvement in expected return above a "do nothing" scenario (Fig. 3c). A 10% reduction in fitness produced relatively similar results to no outbreeding depression; however, a 50% reduction in fitness often vastly increased the probability of extinction, and the diversity measure D), resulting in a reduced expected return. Simulation runs that coupled the maximum reproductive rate with a high carrying capacity were able to withstand high levels of outbreeding depression (S3). Across all remaining parameter sets, increasing the level of outbreeding depression generally tightened the window of opportunity in which to conduct TGF actions in an optimal way (e.g. Figure 2b). Across all scenarios higher levels of outbreeding depression reduced the expected return (Fig. 4a), though the expected return was rarely worse than a "do nothing" scenario. These loses were partly combatted by higher levels of trait heritability within a population. The optimal management action was influenced by the level of outbreeding depression in the system, with high levels of outbreeding depression resulting in an apparently random optimum (Fig. 4b). This is due to only tiny (if any) differences in the expected return across the management landscape coupled with the model's inherent stochasticity (Fig. 3c).

## Discussion

Our model reveals that our chosen management objective—to maximise the remaining genetic diversity of the recipient population at the end of the management horizon—is sensitive to the timing and size of a given translocation action. There is a clear trade-off between maintaining local allelic diversity, and population persistence. As a general rule, a greater number of introductees in the years surrounding the maximum rate of environmental change reduced the probability of population extinction, but these large cohorts tend to produce a lower retention of the recipient population's alleles. This apparent trade off can be optimised, however, with the highest expected return when we introduce a greater number of pre-adapted individuals immediately prior to when selection is strongest, or by introducing a larger number of individuals earlier. These more optimal strategies give

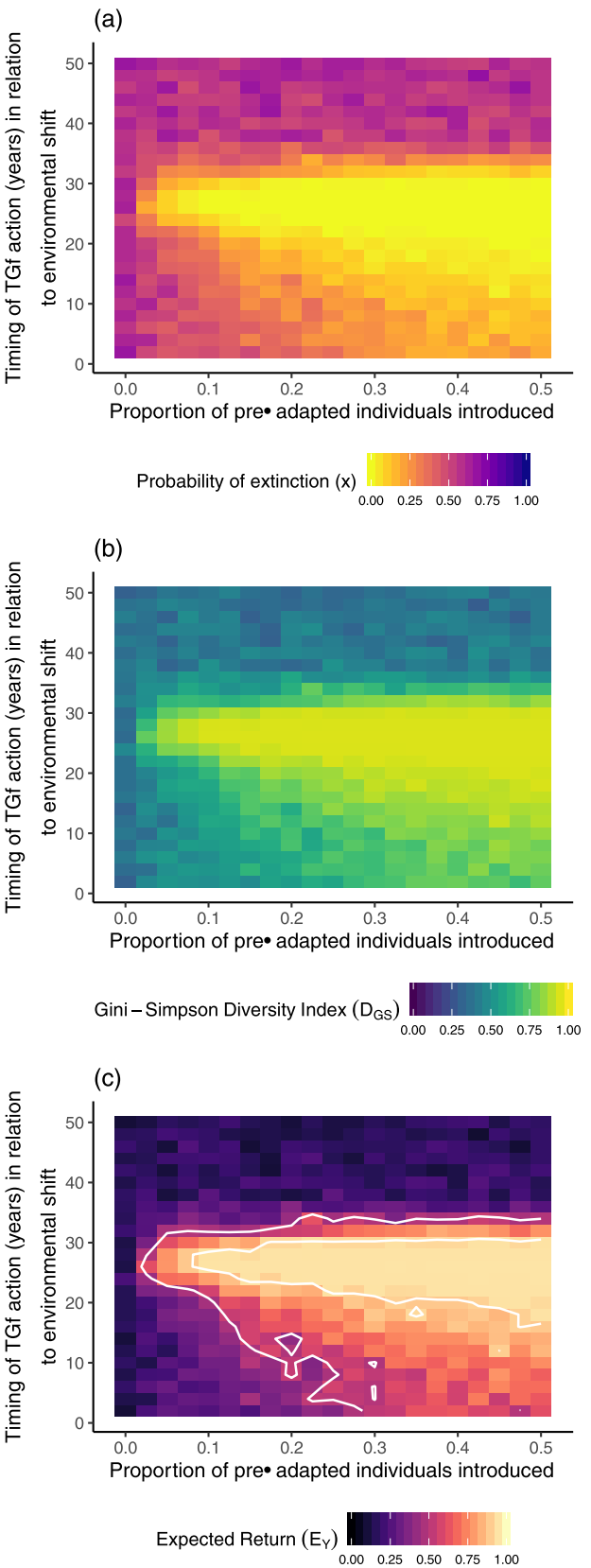


**Fig. 1** Population model results across the management space: varying the timing of targeted gene flow (years) and the proportion of pre-adapted individuals introduced. **a** The probability of extinction ($x$; blue = high chance of extinction) for varying implementations of targeted gene flow; **b** The Gini-Simpson index of diversity ($D$; yellow = high diversity of alleles present) averaged across simulations; and **c** Expected return of management action (i.e. the diversity measure of the surviving population) calculated by $E(Y) = D \cdot (1 - x)$. The bins represent an expected return of 90% (inner) and 50% (outer)

time for recombination to break apart the introduced genome before selection peaks and so retain almost all of the initial allelic diversity.

Our results fit with previous explorations of implementing TGF (with a step-wise threat) (Kelly et al. 2018) or assisted colonisation (that do not consider evolution) which show the timing and size of the introduced cohort to be primary considerations for conservation managers undertaking such actions (McDonald-Madden et al. 2011). Conservationists need not only ensure a species continues to exist, but that the machinery for adaptation remains. Managing extinction risk in partnership with genetic diversity requires the consideration and integration of process such as recombination rate, outbreeding depression, trait heritability and so on, but these must all be considered with future environmental suitability in mind (Naeem et al. 2012). While we found that it is possible to achieve a positive conservation outcome even under harsh levels of environmental change, these more dramatic environmental shifts had a drastically reduced window in which to act and required a much larger introduction size (and hence cost) to achieve an optimal outcome.

The choice of management objective will also influence the optimal course of action. Previous work on TGF has focused on maximising the expected proportion of the recipient genome remaining at the management horizon (Kelly et al. 2018). Here we deepen this idea by considering the allelic diversity rather than allelic richness, by incorporating a measure of diversity—the Gini-Simpson diversity index—into our management objective. This allows us to optimise our actions to ensure not only population persistence and a number of locally adapted alleles are present (richness), but importantly, that the relative abundance at which they occur is relatively even. This evenness can provide a buffer during periods of small population size, slowing the rate at which alleles are lost through drift, so it is important to account for this property. Given that heterozygosity is intrinsically linked to the additive genetic variance, or the ability to respond to environmental change (Falconer and Macaky 1996; Swindell and Bouzat 2005) our reformulated management objective provides an arguably more robust objective with which to optimise gene flow actions. When compared to the earlier metrics, we find that our optimal course did change, usually favouring a delayed course of action, or a larger introduced cohort (S2).

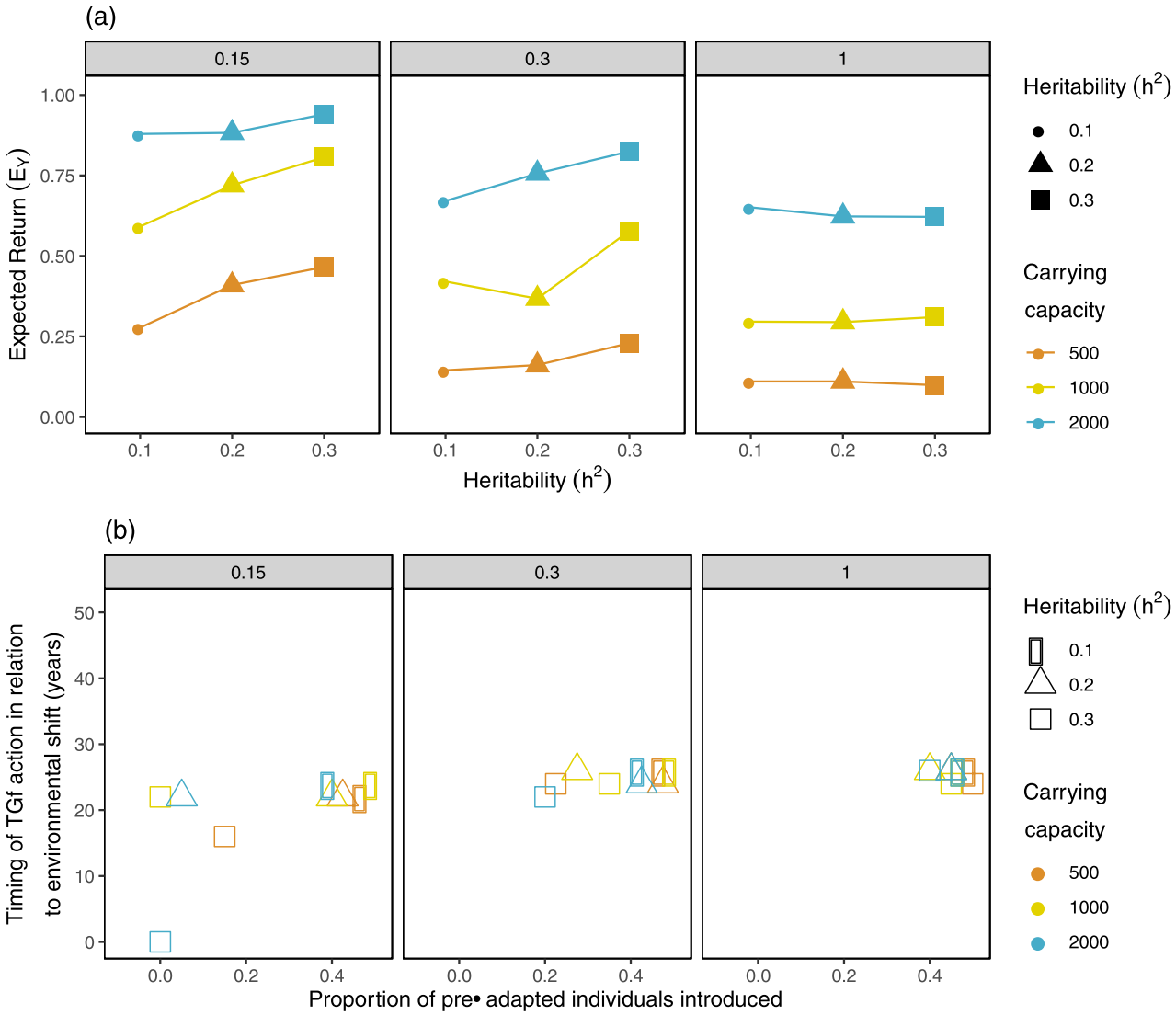


**Fig. 2** Global sensitivity analysis exploring three-dimensional parameter space: carrying capacity ($N^*$: represented by point colours), maximum demographic pressure ($m$: represented in panels) and heritability ($h^2$: represented as point shapes). Showing **a** Maximum expected return (E($Y$)) from a scenario, with outbreeding depression held constant at 10%; **b** displays the location in management space (the timing of targeted gene flow and the proportion of pre-adapted individuals introduced) that produced the maximum expected return (E($Y$) in (a)

Given our management objective, we modelled microevolutionary processes across various scenarios of environmental change to investigate the benefit gained by TGF actions across a range of threat profiles (rates of environmental change). The profiles explored are relevant to threats such as invasive species and disease which may rapidly move into a population and alter it from one state to another (e.g. a near-stepwise change), or climate driven threats which are characterised by a more fluid (and gradual) state change (see S1 for a graphical representation). In general, the greater the rate of environmental shift per timestep, the lower the expected return on a given management action. In addition, the window in which to act is considerably narrower for more rapid threat profiles. Our results suggest that the optimum time of action is usually around the time of most rapid environmental change (regardless of threat profile or other parameters). While the optimum timing is largely unaffected by demographic parameters, these parameters did alter the maximum expected return we could expect.

Despite differences in population dynamics, the optimal strategy for implementing TGF is similar under varying carrying capacities and trait heritabilities. Carrying capacity does, however, have a large bearing on the effectiveness of TGF, with larger populations producing a greater return on investment when compared to small populations. This mirrors theoretical expectations that larger populations can

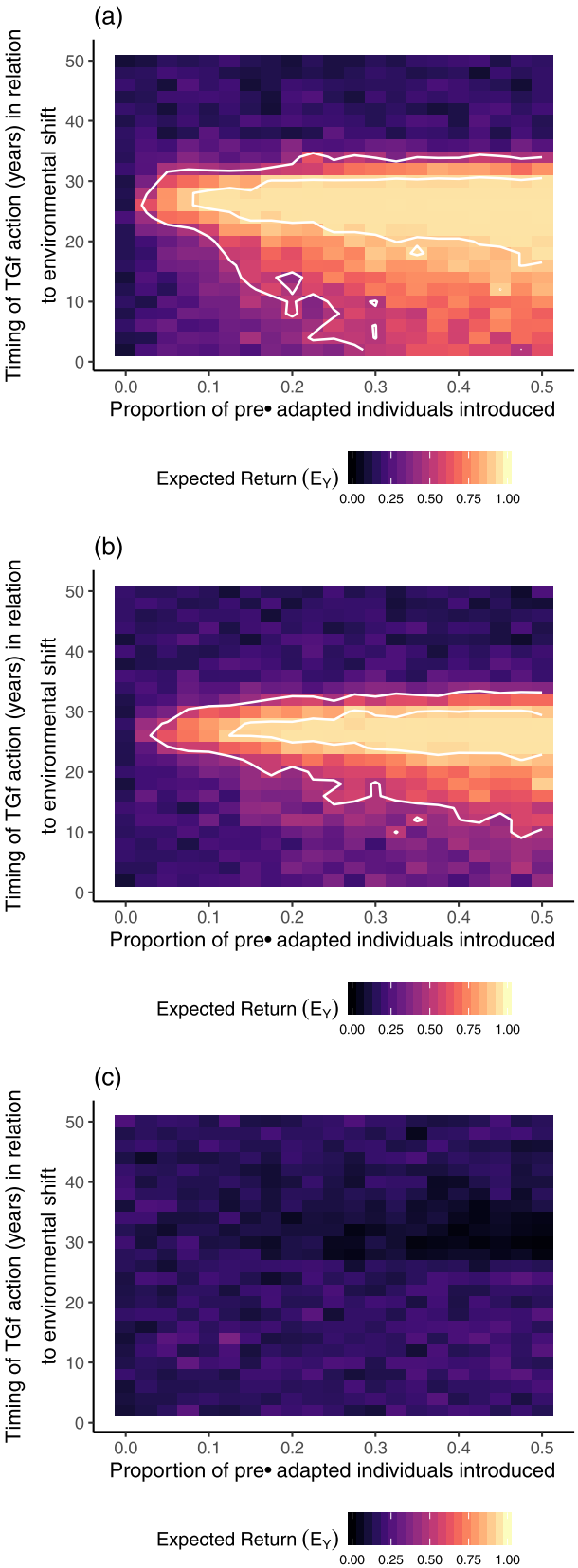


**Fig. 3** Population model results across our management space considering 0% (**a**), 10% (**b**) and 50% (**c**) reduction in fitness for F1 hybrids on the expected return of a management action (i.e. the diversity measure of the surviving population). Bins represent expected return of 90% (inner) and 50% (outer)

evolve more rapidly because they are less affected by stochastic process, such as extinction and genetic drift (Fisher 1930; Wright 1931; Moran 1958). The heritability of the focal trait also affected returns, with less heritable traits causing an increased rate of extinction (particularly when coupled with a high level of outbreeding depression). Overall, TGF decreased extinction probability, and this is consistent across all scenarios.

There is however a risk when hybridising populations (Bell et al. 2019; Harris et al. 2019): outbreeding depression can reduce the population fitness (Frankham et al. 2011). Reduced fitness in hybrids could result from the breakdown of local adaptation, or from genetic incompatibilities such as Dobzhansk-Muller incompatibilities (Fitzpatrick 2008), both of which can be difficult to predict prior to any management action. Our model incorporated the possibility of genetic incompatibilities and showed outbreeding depression reduced the success of TGF. Although it was typically beneficial to act, we uncovered some scenarios with high levels of outbreeding depression in which it was not beneficial to implement TGF. These occur particularly in scenarios where the threat of extinction without intervention is low. Although every management decision has its own peculiarities and risks, recent review suggest that the detrimental effects of outbreeding depression are likely overstated in the literature, and in most cases, outbreeding should cause only minor and transitory effects (see Frankham et al. 2015). By contrast, crossing populations can mask deleterious alleles, and often leads to hybrid vigour, which in turn can lead to a decreased extinction probability (Weeks et al. 2017). The possibility of heterosis (hybrid vigour) is probably as difficult to predict as outbreeding depression: if it occurs in a system it should improve our management objective. Although we don't include heterosis in our model (we are more interested in risks), it should not be forgotten that heterosis is often observed and should improve conservation outcomes under TGF. More generally, any fitness benefits conferred from carrying favourable alleles will likely outweigh transitory impacts of outbreeding depression, and as we found, given time, recombination will ensure that any maladaptive genetic combinations are rapidly lost.

Recombination, by affecting the independence of loci, can potentially lower the effectiveness of TGF. Despite this, we found that increasing the level of recombination had only a mild positive effect on the expected returns but did not change when or how to act. Although the populations survived under various recombination rates, a lower proportion

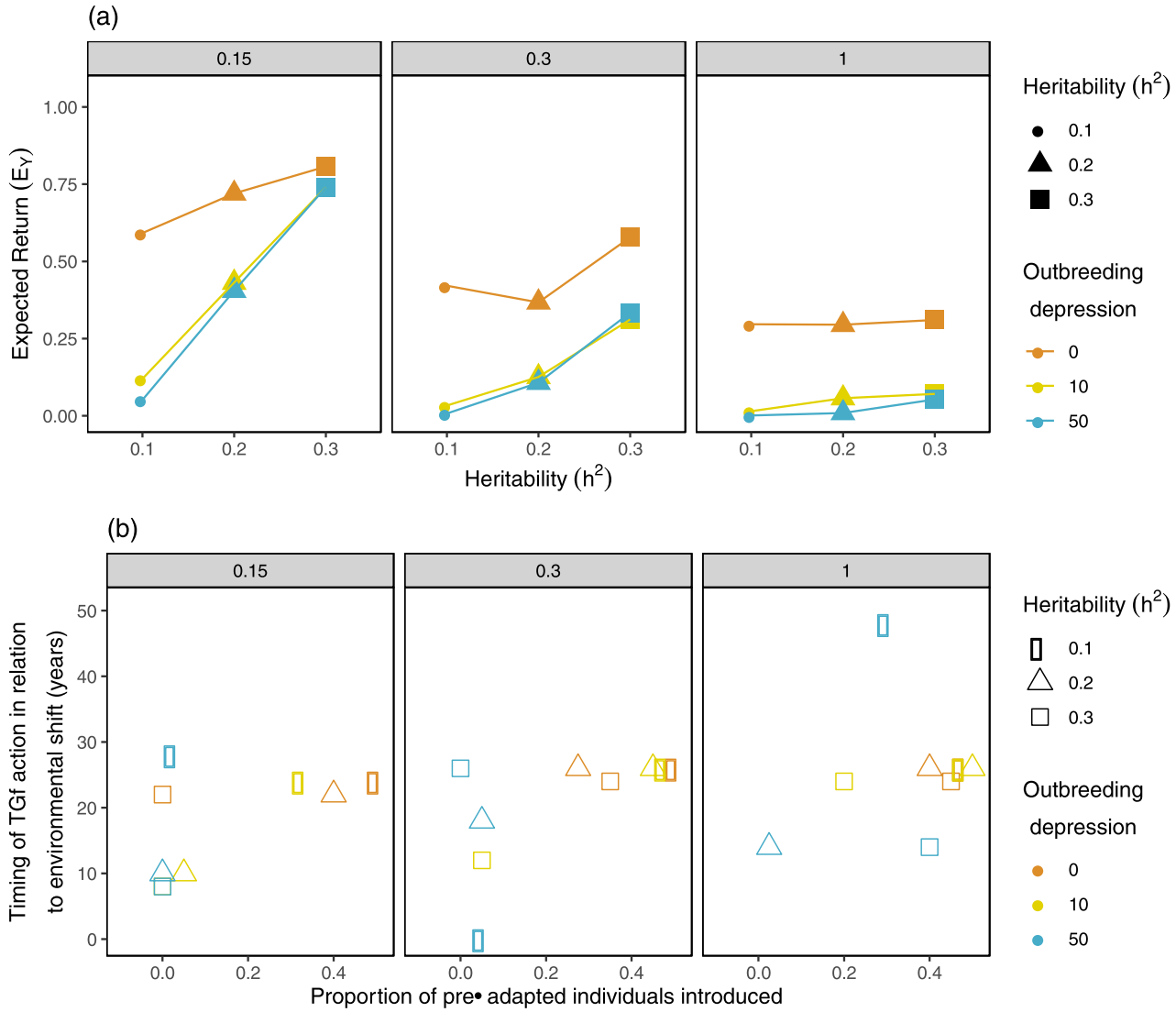


**Fig. 4** Global sensitivity analysis exploring three-dimensional parameter space: outbreeding depression: represented by point colours), maximum demographic pressure (*m*: represented in panels) and heritability ($h^2$: represented as point shapes). Showing **a** Maximum expected return (E(*Y*)) from a scenario, with carrying capacity held constant at 1000 individuals. Part **b** displays the location in management space (the timing of targeted gene flow and the proportion of pre-adapted individuals introduced) that produced the maximum expected return(E(*Y*)) in (a)

of the allelic diversity was retained, because lower recombination rates cause selection to capture larger pieces of the introduced genome: the introduced cohorts' neutral alleles are carried along with the threat-adapted (favoured) alleles. As a precaution, the introduction of threat-adapted individuals should occur as early as feasible to allow time for linkage disequilibrium to decay. Given this advice we found that acting earlier required the introduction or a larger cohort of individuals to obtain a comparable return on investment, which may become an issue if budgets are constrained. Although not explored here, an obvious extension to our work would be to consider multiple introduction events and their relative timing; outcomes in that setting may be quite sensitive to recombination rates.

We, of course, do not capture all possible complexities in our model. In reality, genes influence traits to varying degrees (i.e. there is a distribution of effect sizes, *d*); loci are non-randomly linked; and there are interactions within and between loci (Gomulkiewicz and Holt 1995). Although we have incorporated recombination, and we have integrated over locus positions, reality is far more complex. For example, dominance in phenotypic loci may result in faster adaptive shifts if the dominance effects are in the direction of selection, and this might cause selection

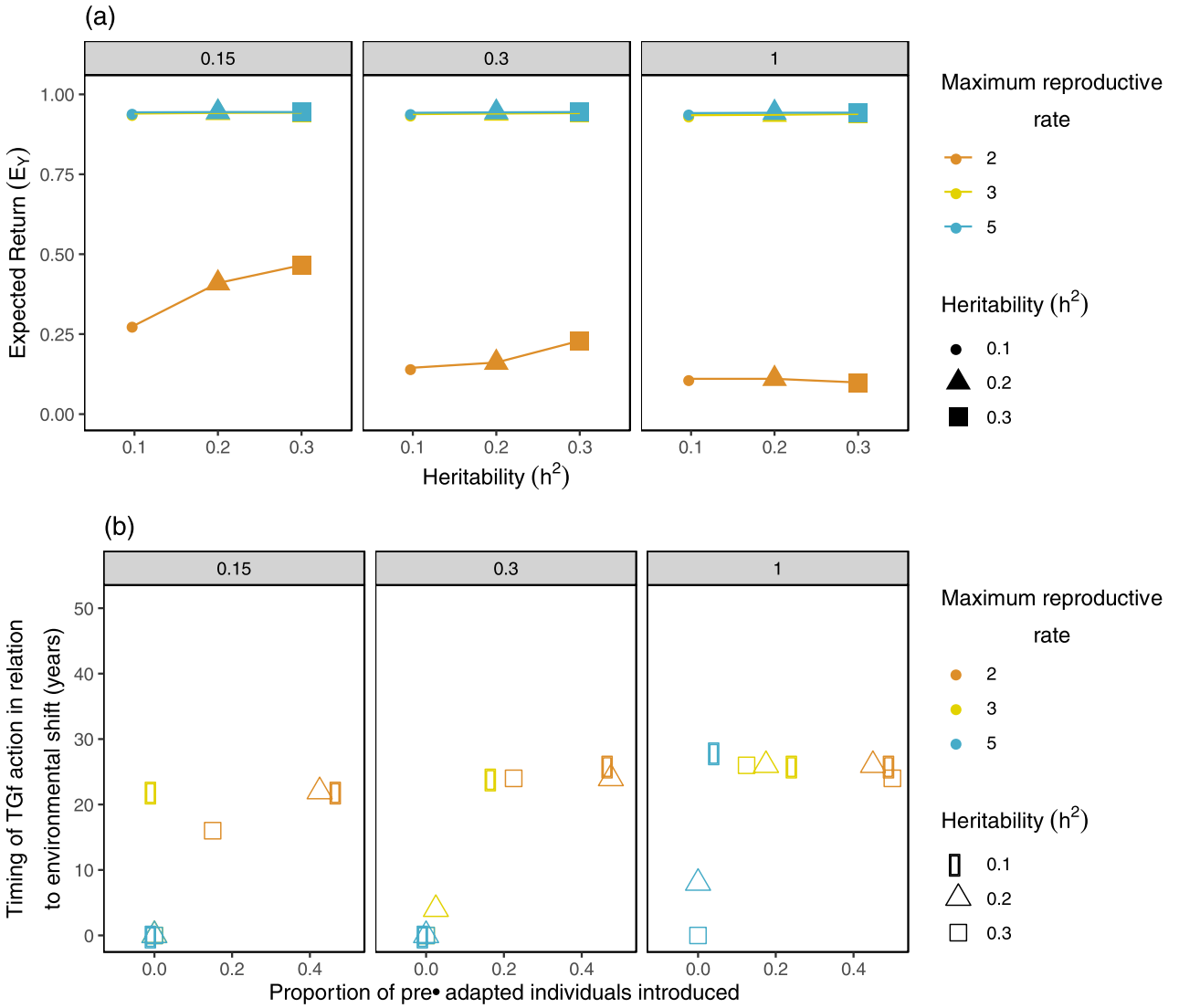


**Fig. 5** Global sensitivity analysis exploring three-dimensional parameter space: reproductive rate: represented by point colours), maximum demographic pressure (*m*: represented in panels) and heritability ($h^2$: represented as point shapes). Showing **a** Maximum expected return (E(*Y*)) from a scenario, with carrying capacity held constant at 1000 individuals. Part **b** displays the location in management space (the timing of targeted gene flow and the proportion of pre-adapted individuals introduced) that produced the maximum expected return(E(*Y*)) in (a)

to fix larger parts of the introduced genome. Dominance may also cause heterosis, and the distribution of dominance effects at phenotypic loci will depend on recent selection pressures on the population. Dominance effects are very likely to be important in TGF, but the distribution of dominance effects is sufficiently uncertain that including them in a model such as ours would likely provide more complexity than clarity. In a real setting it may prove useful to examine composite dominance effects (using F1 crosses, for example) prior to large scale implementation. By quantifying the above points prior to implementation, managers should be confidence on the relative risks and benefits of incorporating TGF into their conservation programs.

As well as being aware of these genetic uncertainties, managers will need to carefully define the accepted levels of final diversity and extinction risk prior to implementing TGF, because these decisions will alter the optimal action. In some cases, incremental gains in diversity or survival probability (for example, from 0.9 to 0.92) will often involve a large increase in effort. Indeed, we found that such gains in diversity or extinction risk do often involve large increases in the size of the introduced cohort. The question then arises, what return on a conservation action

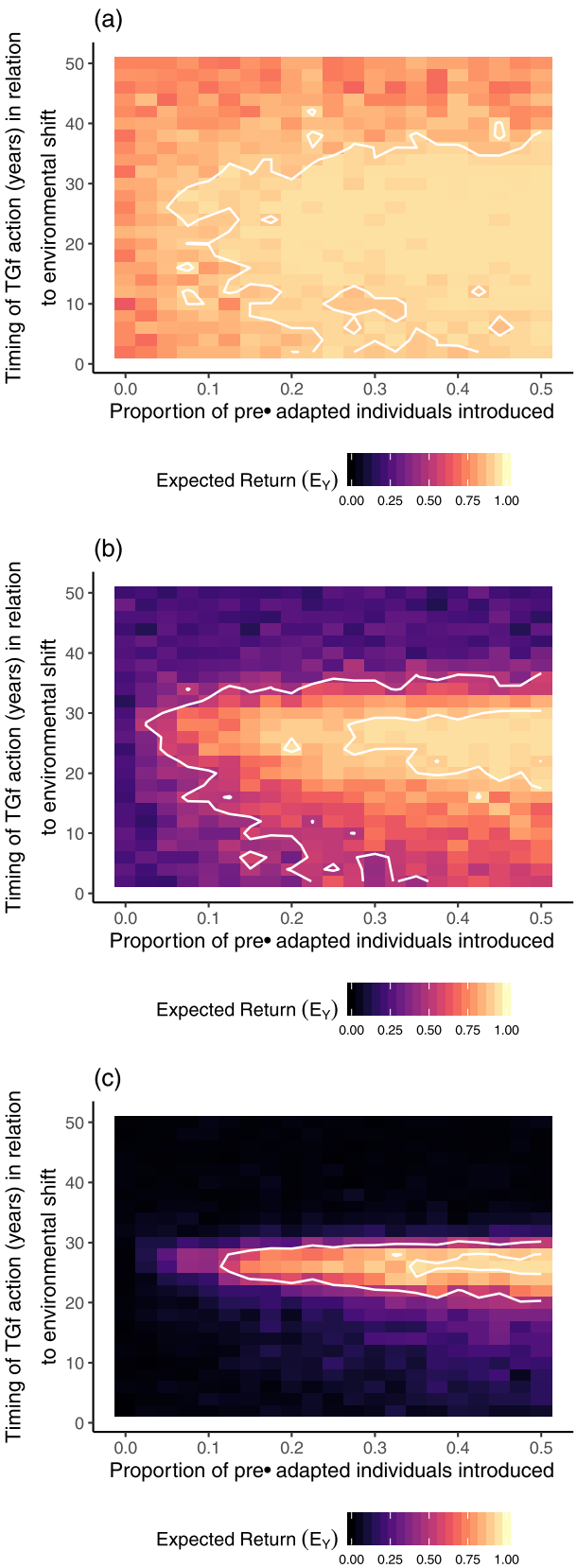


**Fig. 6** Population model results across the management space varying the timing of targeted gene flow (years) and the proportion of pre-adapted individuals introduced. Expected return of a given management action set for a low rate environmental change (m = 0.15) (**a**); a medium level of change (m = 0.3) (**b**); and a severe level of environmental change (m = 1) (**c**). The bins represent an expected return of 90% (inner) and 50% (outer)

is good enough? Given unlimited resources, maximising the objective function makes sense, but given the very real constraints around conservation funding, and competing management actions (e.g., augmentation of existing populations; habitat management; abatement of threats such as predation in situ; fostering connectivity and dispersal; translocation), managers may wish to predefine an acceptable level of benefit that they consider good enough. There are also numerous cases where the need for conservation translocation is immediate (Soorae 2011). Our results suggest that in such cases, a greater number of individuals will be required to achieve even a semi-optimal outcome ($E(Y) >= 0.5$).

Whilst studies examining the optimal implementation of TGF are scarce, one suitable objective function has already been proposed – to maximise the proportion of the recipient genome remaining post TGF action. We extend this earlier objective function into a more holistic measure: the pre-existing allelic diversity remaining post action. Encouragingly, our optimal action sets broadly align with those proposed by the earlier management objective, although when optimising for allelic diversity, the window of action in which to act to affect a positive conservation return is greatly tightened (see S2).

Given this sensitivity it is imperative that management objectives are defined prior to instigating any action. Estimating the timing of intervention requires consideration not only of the biological aspect of conservation decision making but potential delays that result from socioeconomic issues such as budget cycles, permitting, and social licence. For example, a recurrent issue in translocation is that it often involves interagency collaboration, which can be fraught with pitfalls (Susskind 2012). Adding nonbiological issues, like conflict resolution, is likely to increase the urgency for action by increasing the time it takes to act (Wilson 1997; Araiza et al. 2012). In a TGF setting, this will have real costs, often increasing the amount of effort required to achieve a high expected return or missing completely the window of opportunity in which to act. If managers are to adopt TGF into their conservation programs the above uncertainties should be considered, if not empirically assessed.

Although we present a generalised model species here, we recognise that the biology of the species may preclude genetic translocation as a viable alternative. Clearly, a feasibility assessment is warranted early on in the planning process for any real species.

As the impacts of climate change increase, there will be an increased need to translocate populations outside their historic range boundaries and these managed relocation events will require very clear planning and justification (Schwartz and Martin 2013). Although substantially safer than translocation outside the species range, TGF is not without risk. Where individuals are translocated, there is always a risk of translocating pathogens also (Sainsbury and Vaughan-Higgins 2012) that should be considered. Also, there are difficult-to-predict risks associated with placing traits into novel environments (Frankham 2010). The decision to move a trait variant to a new area is not simple. Generally, balancing the needs of a presumptive conservation target against other risks and opportunities is a difficult task. Managers must treat TGF actions as an investment decision (Canessa et al. 2014; McDonald-Madden et al. 2011), and act accordingly. Based on what is known, would TGF be a wise investment of limited resources, or do alternative priorities take precedence? Including this cost-axis into future assessments of TGF presents an important avenue for exploration.

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1007/s10592-023-01541-2.

**Author contributions** AS and BP contributed to all aspects of the manuscript.

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions. This research was supported by an Australian Research Council Future Fellowship to BP (Grant no. FT160100198).

**Data availability** No new data were used in this manuscript. Model code is publicly available from the main authors GitHub repository: https://github.com/assma1/TGFtiming.

## Declarations

**Competing interest** The authors declare no competing interests.



## References

Aitken SN, Whitlock MC (2013) Assisted Gene Flow to facilitate local adaptation to Climate Change. Annu Rev Ecol Evol Syst 44:367–388

Araiza M, Carrillo L, List R, González CAL, Meyer EM, Martínez-Gutiérrez PG et al (2012) Consensus on Criteria for potential areas for Wolf Reintroduction in Mexico: Wolf Reintroduction in Mexico. Conserv Biol 26:630–637

Bell DA, Robinson ZL, Funk WC, Fitzpatrick SW, Allendorf FW, Tallmon DA et al (2019) The exciting potential and remaining uncertainties of genetic rescue. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2019.06.006

Beverton RJH, Holt SJ (1957) On the Dynamics of exploited Fish populations. Springer Science & Business Media, Berlin

Burbidge AA, Byrne M, Coates D, Garnett ST, Harris S, Hatward MW et al (2011) Is Australia ready for assisted colonization? Policy changes required to facilitate translocations under climate change. Pac Conserv Biology 17:259

Canessa S, Hunter D, McFadden M, Marantelli G, McCarthy MA (2014) Optimal release strategies for cost-effective reintroductions. J Appl Ecol 51:1107–1115

Chevin L-M, Hoffmann AA (2017) Evolution of phenotypic plasticity in extreme environments. Philosophical Trans Royal Soc B: Biol Sci 372:20160138

Commander LE, Coates D, Broadhurst L, Offord CA, Makinson RO Matthes M (2018) Guidelines for the translocation of threatened plants in Australia. Third Edition. Australian Network for Plant Conservation, Canberra

Cook CN, Sgrò CM (2017) Aligning science and policy to achieve evolutionarily enlightened conservation: Evolutionary Biology in Policy. Conserv Biol 31:501–512

Cunningham AA (1996) Disease Risks of Wildlife Translocations. Conserv Biol 10:349–353

Falconer DS (1996) In: Mackay TFC (ed) Introduction to quantitative Genetics. Longman, Harlow, UK

Fisher RA (1930) The genetical theory of natural selection. Oxford Clarendon Pres, Oxford

Fitzpatrick BM (2008) Dobzhansky-Muller model of hybrid dysfunction supported by poor burst-speed performance in hybrid tiger salamanders: performance in hybrid salamanders. J Evol Biol 21:342–351

Frankham R (2010) Where are we in conservation genetics and where do we need to go? Conserv Genet 11:661–663

Frankham R (2015) Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Mol Ecol 24:2610–2618

Frankham R, Ballou JD, Briscoe DA (2002) Introduction to conservation genetics. Cambridge University Press, Cambridge

Frankham R, Ballou JD, Eldridge MDB, Lacy RC, Ralls K, Dudash MR et al (2011) Predicting the Probability of Outbreeding Depression: Predicting Outbreeding Depression. Conserv Biol 25:465–475

Ghalambor CK, McKAY JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407

Gomulkiewicz R, Holt RD (1995) When does Evolution by Natural Selection prevent extinction? Evolution 49:201–207

Guiasu RC, Guiasu S (2012) The weighted gini-simpson index: revitalizing an old index of biodiversity. Int J Ecol 2012:1–10

Harris K, Zhang Y, Nielsen R (2019) Genetic rescue and the maintenance of native ancestry. Conserv Genet 20:59–64

Hedrick PW, Fredrickson R (2010) Genetic rescue guidelines with examples from mexican wolves and Florida panthers. Conserv Genet 11:615–626

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. Nature 470:479–485

Hoffmann AA, Sgrò CM, Kristensen TN (2017) Revisiting adaptive potential, Population size, and Conservation. Trends Ecol Evol 32:506–517

Indigo N, Smith J, Webb JK, Phillips B (2018) Not such silly sausages: evidence suggests northern quolls exhibit aversion to toads after training with toad sausages. Austral Ecol 43:592–601
IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change[Masson-Delmotte, VP, Zhai A, Pirani SL, Connors, Péan S, Berger N, Caud Y, Chen L, Goldfarb MI, Gomis M, Huang K, Leitzell E, Lonnoy JBR, Matthews T, Maycock T, Waterfield O, Yelekçi R, Yu B, Zhou (eds)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, In press. https://doi.org/10.1017/9781009157896.
Kelly EL, Phillips B (2018) How many, and when? optimising targeted gene flow for a step change in the environment. Ecol Lett. https://doi.org/10.1111/ele.13201
Kelly E, Phillips BL (2019) Targeted gene flow and rapid adaptation in an endangered marsupial. Conserv Biol 33(1):112–121. https://doi.org/10.1111/cobi.13149
Klein C, Wilson K, Watts M, Stein J, Berry S, Carwardine J et al (2009) Incorporating ecological and evolutionary processes into continental-scale conservation planning. Ecol Appl 19:206–217
Knight AT, Cowling RM, Campbell BM (2006a) An operational model for Implementing Conservation Action. Conserv Biol 20:408–419
Lacy RC (1997) Importance of genetic variation to the viability of mammalian populations. J Mammal 78:320–335
Lacy RC (2019) Lessons from 30 years of population viability analysis of wildlife populations. Zoo Biol 38:67–77
Lafayette L, Sauter G, Vu L, Meade B (2016) Spartan performance and flexibility: an HPC-Cloud chimera. OpenStack Summit, Barcelona
Lande R, Shannon S (1996) The role of genetic variation in Adaptation and Population Persistence in a changing environment. Evolution 50:434–437
McDonald-Madden E, Runge MC, Possingham HP, Martin TG (2011) Optimal timing for managed relocation of species faced with climate change. Nat Clim Change 1:261–265
Moran P (1958) Random processes in genetics. Math Proc Camb Philos Soc 54(1):60–71. https://doi.org/10.1017/S0305004100033193
Morris EK, Caruso T, Buscot F, Fischer M, Hancock C, Maier TS et al (2014) Choosing and using diversity indices: insights for ecological applications from the german Biodiversity Exploratories. Ecol Evol 4:3514–3524
Naeem S, Duffy JE, Zavaleta E (2012) The functions of Biological Diversity in an age of extinction. Science 336:1401–1406
Noble DWA, Radersma R, Uller T (2019) Plastic responses to novel environments are biased towards phenotype dimensions with high additive genetic variation. Proc Nat Acad Sci 116:13452–13461
Nunney L (2016) Adapting to a changing environment: modeling the Interaction of directional selection and plasticity. J Hered 107:15–24
Pavlik B (1996) Defining and measuring success. In: Falk D, Millar C, Olwell M (eds) Restoring diversity: strategies for the reintroduction of endangered plants. Island Press, Washington, pp 127–155
Pavlova A, Beheregaray LB, Coleman R, Gilligan D, Harrisson KA, Ingram BA et al (2017) Severe consequences of habitat fragmentation on genetic diversity of an endangered australian freshwater fish: a call for assisted gene flow. Evol Appl 10:531–550
Ralls K, Ballou JD, Dudash MR, Eldridge MDB, Fenster CB, Lacy RC et al (2018) Call for a paradigm shift in the genetic management of fragmented populations: genetic management. Conserv Lett 11:e12412
Regan HM, Ben-Haim Y, Langford B, Wilson WG, Lundberg P, Andelman SJ et al (2005) Roust decision-making under severe uncertainty for conservation management. Ecol Appl 15:1471–1477
Sainsbury AW, Vaughan-Higgins RJ (2012) Analyzing Disease Risks Associated with Translocations: *Disease Risk and Translocation*. Conserv Biol 26:442–452
Schwartz MW, Martin TG (2013) Translocation of imperiled species under changing climates: translocation of imperiled species under changing climates. Ann N Y Acad Sci 1286:15–28
Soorae PS (2011) Global re-introduction perspectives: 2011. More case studies from around the globe. IUCN/SSC Re-Introduction Specialist Group*:* 250. IUCN/SSC Re-Introduction Specialist Group and Abu Dhabi, UAE: Environment Agency-Abu Dhabi. Gland, Switzerland
Susskind L, Camacho AE, Schenk T (2012) A critical assessment of collaborative adaptive management in practice: *collaborative adaptive management*. J Appl Ecol 49:47–51
Swindell WR, Bouzat JL (2005) Modelling the adaptive potential of isolated populations: experimental simulations using drosophila. Evolution 59:2159–2169
Team RC (2016) R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
Tingley MW, Monahan WB, Beissinger SR, Moritz C (2009) Birds track their grinnellian niche through a century of climate change. Proc Nat Acad Sci 106:19637–19643
Turelli M, Orr HA (2000) Dominance, epistasis and the Genetics of Postzygotic isolation. Genetics 154:1663–1679
Vallee L, Hogbin L, Monks L, Makinson B, Matthes M, Rossetto M (2004) Guidelines for the translocation of threatened plants in Australia. Australian Network for Plant Conservation, Canberra, Australia
Waller DM (2015) Genetic rescue: a safe or risky bet? Mol Ecol 24:2595–2597
Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, Miller KA et al (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective: translocations in changing environments. Evol Appl 4:709–725
Weeks AR, Stoklosa J Hoffmann AA (2016) Conservation of genetic uniqueness of populations may increase extinction likelihood of endangered species: the case of Australian mammals. Front Zool 13:31. https://doi.org/10.1186/s12983-016-0163-z
Weeks AR, Heinze D, Perrin L, Stoklosa J, Hoffmann AA, van Rooyen A, Kelly T, Mansergh I (2017) Genetic rescue increases fitness and aids rapid recovery of an endangered marsupial population. Nat Commun. 208(1):1071. https://doi.org/10.1038/s41467-017-01182-3
Wilson MA (1997) The wolf in Yellowstone: Science, symbol, or politics? Deconstructing the conflict between environmentalism and wise use. Soc Nat Resour 10:453–468
Wright S (1931) Evolution in mendelian populations. Genetics 16:97–159