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

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Abstract

Targeted gene flow is an emerging conservation approach which involves introducing a cohort of individuals with particular traits to locations where they can effect 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 a given 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.

Introduction

Widespread and rapid environmental change is forcing many species to drastically alter how they interact with and respond to the environment (Hoffman & 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 2015). It is, however, increasingly difficult for populations to shift their range because many plant and animal species are now in fragmented habitat and do not possess the dispersal ability to navigate between suitable patches (Tingley *et al* . 2009). 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 & Hoffman 2017; Noble*et al* . 2019). Genetic adaptation is clearly the most robust solution to directional environmental change, and for populations with suitable standing genetic variation, rapid adaptation may forestall extinction through evolutionary rescue (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 (Lacey 1997; Hoffman *et al.* 2017).

One way to increase the chance of evolutionary rescue is to provide populations with the genetic variation necessary for adaptation. Some strategies advocate simply increasing genetic variation, in a non-directional manner. Such "genetic rescue" is particularly powerful when populations have low diversity and are suffering inbreeding depression (Lande & Shannon 1996; Hedrick & 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 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 (hereafter TGF) with the aim of increasing the frequency of pre-adapted traits in threatened populations (Aitken *et al.* 2013; Kelly & Phillips 2016, 2018; Weeks *et al.* 2017; Indigo *et al.* 2018).

As with any conservation action, TGF carries both risk and cost. 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 & 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) While conservation managers regularly use population models to assess alternative scenarios, adaptive evolutionary processes are rarely included in models of population viability (Lacey 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 translocations are usually to create or maintain viable populations of a single, focal species, with measures of success based on abundance, extent, resilience, persistence, or any combination of the above (Pavlik 1996; Vallee *et al.* 2004). With TGF we also want a viable population, but we want to avoid swamping the local genome in the process. Swamping the local genome 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 (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)). 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. 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). 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 & Guiasu 2012; Morris *et al.* 2014), where 1 represents maximum diversity, and 0, no diversity. Thus our objective is to maximise the expected return:

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 (the timing and size of the introduced cohort) influence the expected return of a TGF action? 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 2018), 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 & Holt 1957)) and a fitness multiplier which yields an individual's expected reproductive output (see S5 for further detail.).

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

Each individual is treated as a sexual hermaphrodite and has a chance to breed with a randomly selected mate. 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.

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. 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.

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:

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

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.

$$z_i \sim N(E\left(z_i\right),\ V_E) \quad (2)$$

The changing environment

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

$$v_M = \frac{c}{1+e^{-m(t-\frac{t}{2})}} \quad (3)$$

where the upper asymptote, c , is the distance from the initial trait mean measured in standard deviations of the initial phenotype distribution (at initialisation, $V_T = 1$). We set this to two across all simulations. The rate at which the environmental suitability moves 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,

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

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 :

$$\frac{\mathrm{dw}}{\mathrm{dt}} = \frac{c \bullet e^{2(km)}}{\left(1-e^{m(t-25)}\right)^2}$$

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

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

It is clear that this maximum pressure can be modified by changing either the absolute magnitude of shift (c) or the flattening constant, m . 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 & 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_H . We use our set of $n_c$incompatibility loci to calculate these values of p for each individual. Following Turelli and Orr, the hybrid breakdown score is given as

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

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.

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:

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

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 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. 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 (described in S5), 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^* .

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 (Figure 1 and 3). The management objective (E(Y)) was optimised when a greater proportion of individuals (>10%) 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 (Figure 2, 4 and 5).

Trait heritability (h^2) impacts the success of our simulated management actions. Higher heritabilities increased the expected return, with particular respect to scenarios where there is a lower carrying capacity (Figure 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 (Figure 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 (Figure 2b).

The chosen shape of environmental shift changed the maximum expected return as well as the optimal location in management space (timing and size) (Figure 6). Scenarios with a gradual environmental shift produced a higher expected return than scenarios with a severe 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 (Figure 1c, 3a, b).

Outbreeding depression drastically reduced the success of TGF, in some cases generating no improvement in expected return above a "do nothing" scenario (Figure 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 our diversity measure, 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). Higher levels of outbreeding depression reduced the expected return (Figure 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 our outbreeding depression resulting in an apparently random optimum (Figure 4b). This is due to only tiny differences in the expected return across the management landscape coupled with the model's inherent stochasticity (Figure 3c).

Discussion

Our model reveals that our chosen management objective – to maximise the remaining genetic diversity of the recipient population – 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 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). 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. 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 to achieve an optimal outcome.

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 (D) 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 & Macaky 1996; Swindell & 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).

We modelled microevolutionary processes across various scenarios of environmental change to investigate the benefit gained by TGF actions across a range of threat profiles. The profiles explored (see S1) 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 state change. 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. While the optimum timing is largely unaffected by demographic parameters, these parameters did alter the maximum expected return we could expect.

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 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; Haris *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 (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 is probably as difficult to predict as outbreeding depression: if it occurs in a system its effects should be to improve our management objective. Although we don't include heterosis in our model, 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 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 & Holt 1995). Although we have incorporated recombination, and we have integrated over locus positions, reality is far more complex. 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 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.

Managers need to carefully define the accepted levels of final diversity and extinction risk prior to implementing TGF. 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 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 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; Ariza *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. 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. 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 & Vaughan-Higgins 2012) that should be considered. Also, there are difficult-to-predict risks associated with placing traits into novel environments. 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.* 2012) 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 targeted gene flow presents an important avenue for exploration.

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Figures and Tables.

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Figure 1.

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Figure 2.

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Figure 3.

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of-environmental-change

Figure 4.

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Figure 5.

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Figure 6

Figure captions.

Figure 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).

Figure 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).

Figure 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).

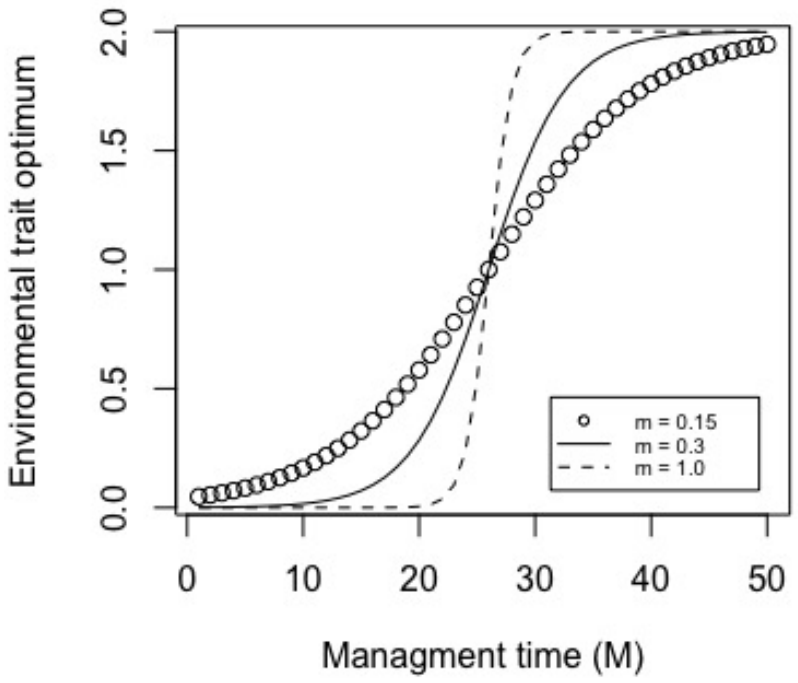
Figure 4. Global sensitivity analysis exploring three-dimensional parameter space: outbreeding depression: represented by point colours), maximum demographic pressure (m : represented in panels) and heritability (h^2 : represented as point shapes). Showing (a) Maximum expected return (E(Y)) from a scenario, 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).

Figure 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).

Figure 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).

Supplementary Material Figures



Supplementary Figure 1.

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Supplementary Figure 2.

Supplementary Material Captions

S1: Plot of the modelled environmental optimum over time for varying implementations of, m . The three lines represent m values of 0.15 (dotted), 0.3 (line) and 1 (dashed).

S2: Comparison of two potential management objectives showing: a) our management objective, the survival of the recipient populations allelic diversity, measured via the Gini-Simpson Index; and b) the survival of the recipient populations genome (described by Kelly & Philips 2018).

S3: Full graphical output of the explored parameter space showing each factorial pairwise combination. The numbers in the top left correspond to the input values for that particular parameter set (see S5) in the

following order: initial frequency of alleles, the recombination rate, trait heritability, maximum reproductive rate, carrying capacity, maximum demographic pressure and outbreeding depression. Available via online GitHub repository only.

S4: Full coding implementation of the model described in Smart & Phillips (2019): Optimizing targeted gene flow to maximize local genetic diversity: when and how to act under various scenarios of environmental change. Available via online GitHub repository only.

S5. Supplementary methods, including details surrounding the global sensitivity analysis and management scenarios.