







## CONTRIBUTED PAPER

# The immediate costs and long-term benefits of assisted gene flow in large populations

Jared A. Grummer<sup>1</sup>  | Tom R. Booker<sup>1,2</sup>  | Remi Matthey-Doret<sup>1,3</sup>  |  
Pirmin Nietlisbach<sup>1,4</sup>  | Andréa T. Thomaz<sup>1,5</sup>  | Michael C. Whitlock<sup>1</sup> 

<sup>1</sup>Biodiversity Research Centre and Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada

<sup>2</sup>Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada

<sup>3</sup>Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

<sup>4</sup>School of Biological Sciences, Illinois State University, Normal, Illinois, USA

<sup>5</sup>Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia

## Correspondence

Jared A. Grummer, Biodiversity Research Centre and Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, BC V6T 1Z4, Canada.

Email: [grummer@zoology.ubc.ca](mailto:grummer@zoology.ubc.ca)

Jared A. Grummer, Tom R. Booker, Remi Matthey-Doret, Pirmin Nietlisbach, and Andréa T. Thomaz contributed equally to this work.

**Article impact statement:** Assisted gene flow can aid adaptation and improve the genetic health or fitness of a population, but usually the effect is small or delayed.

## Abstract

With the genetic health of many plant and animal populations deteriorating due to climate change outpacing adaptation, interventions, such as assisted gene flow (AGF), may provide genetic variation necessary for populations to adapt to climate change. We ran genetic simulations to mimic different AGF scenarios in large populations and measured their outcomes on population-level fitness to determine circumstances in which it is worthwhile to perform AGF. In the absence of inbreeding depression, AGF was beneficial within a few generations only when introduced genotypes had much higher fitness than local individuals and traits affecting fitness were controlled by a few genes of large effect. AGF was harmful over short periods (e.g., first ~10–20 generations) if there was strong outbreeding depression or introduced deleterious genetic variation. When the adaptive trait was controlled by many loci of small effect, the benefits of AGF took over 10 generations to realize—potentially too long for most climate-related management scenarios. The genomic integrity of the recipient population typically remained intact following AGF; the amount of genetic material from the donor population usually constituted no more of the recipient population's genome than the fraction of the population introduced. Significant genomic turnover (e.g., >50% replacement) only occurred when the selective advantage of the adaptive trait and translocation fraction were extremely high. Our results will be useful when adaptive management is used to maintain the genetic health and productivity of large populations under climate change.

## KEYWORDS

assisted migration, conservation genetics, local adaptation, migration pulsing, outbreeding depression, translocation

## Resumen

Con el deterioro de la salud genética de muchas poblaciones de plantas y animales debido a la ventaja que le lleva el cambio climático a la adaptación, algunas intervenciones, como el flujo génico asistido (FGA), pueden proporcionar la variación genética necesaria para que las poblaciones se adapten al cambio climático. Simulamos diferentes escenarios de FGA aplicado en poblaciones grandes y medimos los resultados en la aptitud a nivel poblacional para determinar las circunstancias en las que merece la pena realizar FGA. Cuando no hubo depresión endogámica, el FGA produjo un beneficio en pocas generaciones sólo cuando se introdujeron genotipos que tenían una aptitud mucho mayor que los individuos locales y cuando unos cuantos genes de gran efecto controlaron los rasgos que afectaban a la aptitud. El flujo génico asistido fue dañino en periodos cortos (p.ej.: las primeras 10–20 generaciones) si existía una fuerte depresión exogámica o una variación genética deletérea introducida. Cuando muchos loci de pequeño efecto controlaron el rasgo adaptativo, los beneficios del FGA tardaron más de 10 generaciones en aparecer – un tiempo potencialmente muy largo para la mayoría de la gestión relacionada con el clima. La

integridad genómica de la población receptora casi siempre permaneció intacta después del FGA; es decir, la cantidad de material genético de la población donante generalmente no constituyó más que la fracción de población introducida en el genoma de la población receptora. La rotación genómica significativa (p.ej.: reemplazos >50%) sólo ocurrió cuando la ventaja selectiva del rasgo adaptativo y la fracción de reubicación fueron extremadamente elevadas. Nuestros resultados serán útiles cuando se use la gestión adaptativa para mantener la salud genética y la productividad de las poblaciones grandes bajo el cambio climático.

#### PALABRAS CLAVE:

adaptación local, depresión exogámica, genética de la conservación, migración asistida, migración latente, reubicación

## INTRODUCTION

Natural populations face many anthropogenic threats (e.g., climate change, habitat loss) that can lead to fitness reductions and population declines (Klenner & Arsenault, 2009; Pacifici et al., 2017). In the face of environmental change, local populations can migrate, adapt, exhibit phenotypic plasticity, or become extinct (Hamilton & Miller, 2016). Migration is not possible for many species due to habitat fragmentation (Hoffman & Sgrò, 2011). Phenotypic plasticity may provide temporary relief (Levis & Pfennig, 2016), but sometimes plastic responses are harmful over time (Oostra et al., 2018). Populations can adapt through natural selection, but rapid anthropogenic environmental change often outpaces adaptation (e.g., Gonzalez et al., 2013; Radchuk et al., 2019; Wilczek et al., 2014). Adaptation requires genetic variation on which to act, but that variation may be lacking in certain populations.

Many keystone and economically relevant species have been studied for their capacity to adapt to changing climates (Anderson, 2016). Corals, often keystone species in marine communities, are under threat from ocean acidification and rising temperatures (Baker et al., 2008). In some coral species, natural populations respond differently to these threats (Hughes et al., 2003), suggesting that gene flow from other populations may benefit populations subject to climate warming and ocean acidification. Genomic data and biophysical modeling suggest that gene flow from lower to higher latitude coral populations could provide beneficial heat-tolerant alleles as the climate warms (Matz et al., 2018). Furthermore, accounting for genetic and climatic effects when planting lodgepole pine (*Pinus contorta*) could increase harvests (Wang et al., 2010). Similarly, Norway spruce (*Picea abies*) and silver fir (*Abies alba*) might be maladapted to future environmental conditions (Frank et al., 2017), potentially affecting their ecological functions and protection of towns from avalanches and mudslides. Gene flow from plant populations in drier regions could help populations in mesic regions predicted to experience more frequent droughts (e.g., Exposito-Alonso et al., 2018). Recent increases in habitat fragmentation (Grill et al., 2019; Haddad et al., 2015) will likely inhibit the natural process of adaptation via gene flow.

Assisted gene flow (AGF), i.e., human-mediated and intentional translocation of individuals within a species range to facilitate adaptation to anticipated local conditions, has been pro-

posed to introduce genetic variation into populations potentially facing fitness declines via maladaptation (e.g., Aitken & Whitlock, 2013; Tomasini & Peischl, 2020; Uecker et al., 2014). Ultimately, AGF is typically invoked to increase adaptability of populations threatened by climate change in the present or near future. A population's rate of adaptation is proportional to the extent of genetic variation it harbors (Walsh & Lynch, 2018). AGF attempts to increase the genetic variation of a population to buffer it against the effects of changing climates. Other types of assisted migration move individuals outside current ranges, whereas AGF refers to translocations among existing populations.

AGF is distinct from genetic rescue. Genetic rescue is an increase in the fitness of small populations owing to immigration of new alleles (Tallmon et al., 2004) and is generally considered to occur when population fitness increases by more than the demographic contribution of immigrants (Ingvarsson, 2001), although broader definitions of genetic rescue exist (e.g., Hufbauer et al., 2015). Although the goal of genetic rescue is to prevent a population from going extinct, AGF's potential applications are broader. For instance, AGF can affect the spatial distribution of genetic variation and population size of a species, thereby potentially affecting ecosystem function and stability (Balmford et al., 2003; Luck et al., 2003). Thus, while AGF can be used to prevent extinction of threatened species, it can also increase population health of keystone species and promote productivity in economically important species (e.g., Aitken & Bemmels, 2016).

In this study, we focused on large populations not experiencing high levels of inbreeding depression. AGF is typically invoked as a conservation action when a population is, or will be (based on projected future climates), no longer adapted to its environment. When performing AGF, individuals harboring preadaptive alleles—alleles that cause local adaptation to a particular environmental trait—are translocated to imperiled populations (Aitken & Whitlock, 2013).

Introducing genotypes from foreign sources poses risks to a population's fitness and genetic integrity. The aim of AGF may be to aid adaptation to warming temperatures, but if donor populations are, for example, adapted to different seasonal cycles and exhibit phenological mismatch at the new location, population fitness may be reduced. Furthermore, introduced genetic variation may generate negative epistatic interactions with local

alleles (i.e., outbreeding depression [OD] [Frankham et al., 2011; Templeton et al., 1986]). Such locally deleterious alleles—alleles that may be fit elsewhere but unfit in the recipient population—will initially be in strong linkage disequilibrium with beneficial alleles that are introduced, potentially making them even more consequential. It is therefore important to consider the level of OD and environmental differences between donor and recipient populations in assisted migration efforts, but it is currently unclear how these negative effects can reverse or ameliorate AGF's benefits. Another risk of AGF is genetic swamping from hybridization between populations, which can lead to a population's loss of genetic integrity and potentially genomic extinction (Todesco et al., 2016).

Managers have several decisions to make when considering invoking AGF in large populations in terms of migration effort, translocation strategy, and fitness reductions. How many individuals should be translocated? Translocating many individuals to increase the odds of allele frequency change in the recipient population could be expensive. Moreover, the resulting high proportion of foreign individuals in the local population may dilute or completely replace the composition of the recipient gene pool. Conversely, adding too few individuals might not introduce the preadaptive alleles at a high enough frequency to overcome drift and remain in the population.

Should all individuals be translocated at once or over several generations (pulsed strategy)? Population-level fitness can decrease immediately following translocation (Aitken & Whitlock, 2013) and pulsing immigration events can increase the probability of local adaptation in recipient populations (Peniston et al., 2019). Therefore, pulsed translocation could lead to higher population-level fitness relative to a single translocation event.

Do long-term fitness gains outweigh short-term losses? OD and maladaptive alleles could lead to sharp reductions in population-level fitness following translocation; is this fitness valley so deep that it can impair fitness recovery and potentially lead to local extinction, or is the fitness valley shallow enough to be transcended and ultimately lead to long-term fitness improvements?

We used individual-based simulations to investigate the genetic circumstances that make AGF worthwhile in large populations. We chose a range of values, including extremes for many parameters, to explore when AGF could be the most beneficial or harmful. We assessed the combined effect of alleles that are preadapted to a changing climatic variable (i.e., lead to local adaptation), maladaptive alleles (i.e., alleles fixed in the donor population but deleterious in the recipient population), and alleles that cause OD. We simulated various genetic architectures of these traits that have positive (preadaptation) and negative (maladaptation, OD) consequences on the recipient population's fitness. Population mean fitness was tracked over time to determine how different genetic architectures affected short- and long-term fitness of the recipient population. We considered the implications of these results for natural resource managers and conservation practitioners.

## METHODS

We conducted population genetic simulations with SimBit 4.9.30 (Matthey-Doret, 2021). A glossary of terms and default parameter values is in Table 1. We simulated the translocation of individuals from a donor population to a recipient population of either 1000 or 10,000 diploid individuals. We assumed that the recipient population had been subject to some climate change that caused maladaptation, but that a donor population was fixed for some alleles that were preadapted to respond to that climate change. The donor population was sometimes also fixed for alleles that were maladaptive in the recipient population (details below). The loss of fitness in the recipient population was entirely due to maladaptation caused by climate change; the populations were large enough that inbreeding depression did not meaningfully affect the fitness of the population. We modeled a translocation fraction ( $T_f$ ) of either 5% or 50% ( $T_f = 0.5\%$  results throughout Appendices), meaning that individuals from the donor population made up 5% or 50% of the recipient population, respectively. Although a translocation fraction of 50% may be unrealistic in some scenarios, it helps visualization of trends of the impact of translocation effort on fitness and local genetic identity. We modeled selection on fecundity, so the first round of selection in all simulations occurred at the time generation 1 was produced.

The frequency of introducing foreign genotypes—whether in a single versus several discrete events—affects the probability of allelic fixation and therefore local adaptation (Aubree et al., 2021; Peniston et al., 2019). We therefore examined the effect of introduction strategy on population mean fitness by modeling translocation in a single pulse or in 5 pulses separated by 1, 2, or 4 generations, each pulse representing 20% of the total number of individuals translocated. The number of pulses was chosen to be somewhat large to maximize its effect in the simulations, but low enough to be practical for management. We expected qualitative conclusions to be similar with fewer or more pulses. After the introduction, the simulated recipient population evolved for 100 generations.

We modeled alleles that were locally preadapted and maladapted to the climate of the recipient population. We modeled alleles that were selectively favored in the donor population (and fixed there). Some of these alleles were adaptive in the new environment of the recipient population (preadapted alleles) and others had low fitness in the new environment (maladaptive alleles). We assumed these alleles were fixed (e.g., frequency = 1.0) in the donor population and absent in the recipient population until introduced by AGF, indicating that populations were only distantly related. This case of extreme allele frequency differences allowed demonstration of AGF's maximal effects.

We parameterized the selective effects of preadaptive and maladaptive alleles by focusing on the overall effect of 0, 1, 5, or 50 selected loci. If an individual in the recipient population was homozygous for all preadaptive (PA) alleles, its relative fitness would be increased by  $\Delta_{PA}$ . Similarly, if an individual in the recipient population was homozygous for all maladaptive (MA) alleles, its relative fitness would be decreased by  $\Delta_{MA}$ . We

**TABLE 1** Glossary of terms and parameters used in an examination of assisted gene flow

Term	Definition	Values used in simulations
Assisted gene flow (AGF)	Process of translocating individuals to increase frequency of beneficial alleles in the recipient population	
Donor population	Population that supplies individuals for translocation	
Recipient population	Population that receives translocated individuals	
Local genomic replacement (LGR)	Proportion of recipient genome derived from alleles introduced from the donor population (averaged across all individuals in population)	
Translocation fraction ( $T_f$ )	Proportion of recipient population replaced by translocated individuals at time of introduction	0.5%, 5%, 50%
Translocation pulses	Number of discrete translocation events	Single pulse or 5 pulses each comprising 20% of $T_f$ every 1, 2, or 4 generations
Recipient population size	Number of diploid individuals in recipient population (remains constant)	1000, 10,000
Preadaptive (PA) alleles	Preadaptive (beneficial) alleles coming from translocated individuals	0, 1, 5, 50
PA dominance coefficient	Dominance of PA alleles	0.5 (i.e., additive gene action)
$\Delta_{PA}$	Maximum possible fitness increase in an individual carrying all preadaptive alleles	0%; 10%; 50%
Maladaptive (MA) alleles	Maladaptive alleles coming from translocated individuals	0; 1; 5; 50
MA dominance coefficient	Dominance of MA alleles	0 (= MA alleles are recessive); 0.5 (= additive gene action)
$\Delta_{MA}$	Maximum possible fitness reduction in an individual carrying all maladaptive alleles	0%; ~9.1%; 50%
Outbreeding depression (OD) loci	Pairs of loci with additive-by-additive epistasis	0; 2; 10; 100
$\Delta_{OD}$	Fitness reduction of a genotype heterozygous for all loci relative to local or foreign double homozygotes due to outbreeding depression	0%; 20%; 60%
Neutral loci	Neutral loci used to calculate LGR	100

simulated cases with  $\Delta_{PA}$  of 10% or 50% and  $\Delta_{MA} \approx 9.1\%$  and 50%. These  $\Delta_{PA}$  and  $\Delta_{MA}$  values represented the maximum change in fitness (e.g., when an individual was homozygous for all preadaptive or maladaptive alleles). Therefore, for a given  $\Delta_{PA}$  or  $\Delta_{MA}$ , a higher number of loci results in a lower selection coefficient per locus. A  $\Delta_{PA}$  of 10% will compensate  $\Delta_{MA} \approx 9.1\%$  in individuals homozygous for either all PA or MA alleles. The dominance coefficient was 0.5 for PA loci and 0.5 for MA loci (see Appendix S1 for MA loci dominance = 0).

OD poses an additional genetic risk when translocating individuals (Frankham et al., 2011). For example, epistatic interactions may considerably reduce the fitness of some heterozygotes and double homozygotes (Orr, 1995, 1996). At equilibrium, strongly deleterious double homozygotes rarely occur in a population. However, they may occur more commonly in individuals with mixed ancestry from differentiated populations. OD was modeled by simulating pairs of loci with additive-by-additive epistasis. An individual homozygous for either foreign or local alleles at both loci in a pair had fitness of  $1 + s_{OD}$  relative to the double heterozygote (double heterozygote fitness = 1). Individuals homozygous for local alleles at 1 locus and foreign alleles at the other had a fitness of  $1 - s_{OD}$  relative to the double heterozygote. All other genotype combinations (i.e., at least 1 heterozygote in a pair) had a fitness of 1.0. We modeled either 0, 2, 10, or 100 pairs of such epistatic OD loci.

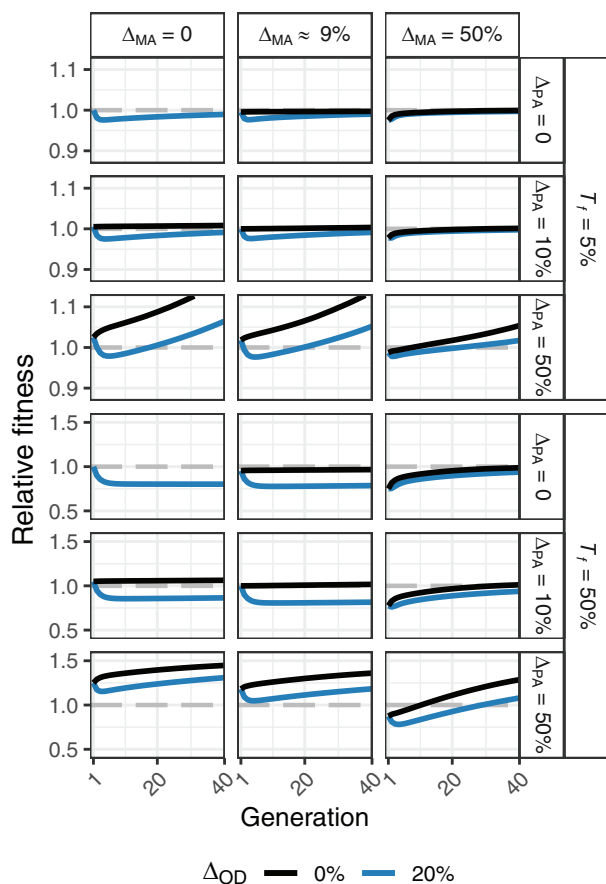
Following Aitken and Whitlock (2013), we parameterized OD by focusing on the overall fitness reduction across all pairs

of loci. Individuals heterozygous for all epistatic pairs had a fitness reduction of  $\Delta_{OD}$  relative to the fittest homozygotes. We simulated cases where OD resulted in fitness reductions of either  $\Delta_{OD} = 20\%$  or  $60\%$  in heterozygotes relative to the fittest double homozygotes. For example, when simulating  $\Delta_{OD} = 20\%$  across 2 pairs of epistatic loci,  $s_{OD} \approx 0.1180$ , for 10 pairs  $s_{OD} \approx 0.0226$ , and for 100 pairs  $s_{OD} = 0.0022$ . A  $60\%$  fitness reduction resulted from 2 pairs of epistatic loci with  $s_{OD} \approx 0.5811$ , 10 pairs with  $s_{OD} \approx 0.0960$ , or 100 pairs with  $s_{OD} \approx 0.0092$ . A  $\Delta_{OD}$  of  $60\%$  is unlikely in intraspecific population pairings (i.e., in most cases where AGF would be considered); we used it as an extreme case to discover when AGF might prove harmful. We therefore present results of only  $\Delta_{OD} = 0\%$  and  $20\%$  in the main text and  $\Delta_{OD} = 60\%$  in the Supporting Information.

For the simulation results presented in the main text, we assumed multiplicative fitness effects among loci and additive interactions between alleles within loci. Fitness effects of OD loci pairs also interacted multiplicatively with all other pairs of PA and MA loci. All loci were randomly distributed onto 10 chromosomes of 10 centimorgans each with a uniform recombination rate. Thus, pairs of loci causing OD were randomly distributed in the genome and therefore often not closely linked.

Local genomic replacement (LGR) may occur as introduced haplotypes spread to fixation in the recipient population, replacing local genetic diversity. Given concerns that an increase in local fitness may be due to a proportionate change in nonlocal





**FIGURE 1** Mean fitness of the recipient population following a single translocation event as a function of  $\Delta_{MA}$  (maximum possible fitness reduction in an individual carrying all maladaptive alleles),  $\Delta_{PA}$  (maximum possible fitness increase in an individual carrying all preadaptive alleles),  $\Delta_{OD}$  (fitness reduction of a genotype heterozygous for all loci relative to local or foreign double homozygotes due to outbreeding depression), and  $T_f$  (translocation fraction). Genomes included 10 pairs of outbreeding depression loci, and where preadaptive and maladaptive alleles occurred, 5 of each were present with variable selection strengths in both  $\Delta_{PA}$  and  $\Delta_{MA}$  (maladaptive allele dominance = 0.5) (gray dashed line, relative fitness of 1.0). Scale of the y-axis differs for different values of  $T_f$ , and x-axes only show first 40 generations. Cases with  $\Delta_{PA} = \Delta_{MA} = 0$  were not simulated and are not shown (relative fitness stays at 1.0).

ancestry (e.g., Harris et al., 2019), we measured local genomic replacement by randomly placing 100 neutral loci in the genome that were reciprocally fixed in source and recipient populations. At every generation, we calculated the mean allele frequency across all neutral markers to obtain a measure of the average proportion of alleles in the local population that derived from alleles introduced during AGF. Our measure of LGR varies from 0 to 1.0, where 1.0 indicates that all neutral alleles in the recipient population are derived from the donor population.

For each combination of all parameter values summarized in Table 1, we performed 50 simulation replicates on a total of 1536 unique parameter combinations. We measured relative fitness in the recipient population and calculated mean fitness across replicates. We used the mean frequency of neutral alleles as a measure of local genomic replacement.

Code to perform and analyze the simulations as well as to plot the results are available at <https://github.com/TBooker/Assisted-Gene-Flow>. The results of all our simulations can be

visualized using a Shiny App (<https://shiny.zoology.ubc.ca/whitlock/AGF/>), the code for which is available in the github repository.

## RESULTS

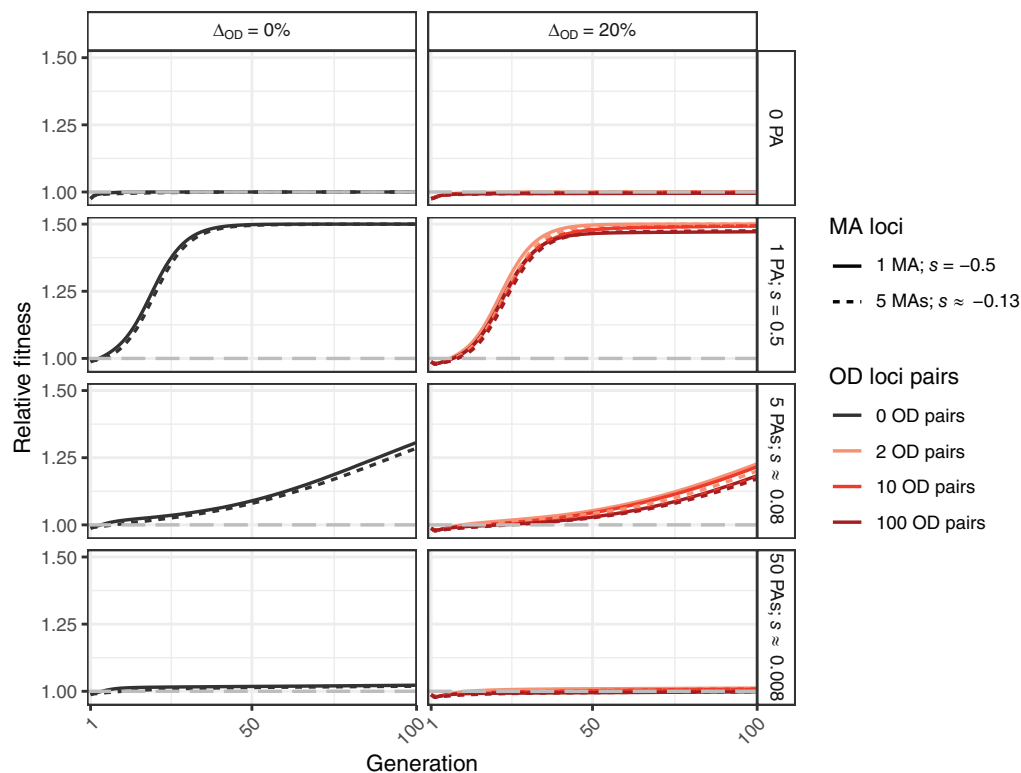
In the absence of maladaptive alleles or OD, introducing preadaptive alleles always increased the fitness of recipient populations (Figure 1). Results from populations of 10,000 individuals and results for populations of 1000 individuals were qualitatively similar (available for exploration in a Shiny app at <https://shiny.zoology.ubc.ca/whitlock/AGF/>). Furthermore, simulations showed little interreplicate variation (Appendix S2), so we present results as the means of 50 simulation replicates per parameter combination.

When OD was present and maladaptation was stronger than the effects of preadaptive alleles, an initial reduction in relative fitness occurred after a translocation replacing 5% of the recipient population. Recipient population fitness typically recovered within 100 generations (often within 20 generations) unless OD was strong and caused by 100 pairs of loci (Figure 1 & Appendix S3). Recovery was even faster with  $T_f = 0.5\%$  (Appendix S4). However, with  $T_f = 50\%$ , fitness recovery could be quite delayed (Figure 1) and did not always recover to pretranslocation levels within 100 generations when OD was  $>0\%$  and maladaptation was weak (Appendix S4). The effect of genetic incompatibilities on fitness mainly depended on the total effect across all loci rather than on the number of pairs of epistatic alleles. For instance, in cases with high migration ( $T_f = 50\%$ ), scenarios with OD of 20% frequently took longer to fully recover than scenarios with OD of 60%, regardless of genetic architecture (Appendix S4).

Fitness-change dynamics after AGF were driven in part by  $\Delta_{PA}$ , the total strength of selection on preadaptive alleles. In the cases where the overall fitness benefit of preadaptive alleles was greater than or equal to the effect of maladaptation, deleterious alleles were purged and preadaptive alleles rose in frequency, increasing population fitness. The presence of maladaptation did not prevent preadaptive alleles from rising in frequency and increasing mean fitness (Figure 1; Appendices S3 & S4). However, when maladaptation was stronger than the fitness benefit of preadaptive alleles, the translocated individuals were purged and AGF had negligible long-term fitness consequences.

The fitness consequences of the interplay between positive and negative selection were dependent on the number of individuals moved (translocation fraction). When the translocation fraction was 5% or smaller (i.e., 0.5%), stronger selection on maladaptive alleles ( $\Delta_{MA}$ ) led to slower fitness recoveries and ultimately to lower fitness increases (Figure 1; Appendices S3 & S4). In the cases of  $T_f = 50\%$ , increasing selection strength on preadaptive alleles led to fewer generations of greatly reduced fitness when selection was weak on maladaptive alleles ( $\Delta_{MA} = 0$ ).

The magnitude of population fitness increase due to AGF was highly dependent upon the genomic architecture underlying the traits of interest. When there was only a single large-effect preadaptive allele, fitness increased to the maximum possible



**FIGURE 2** Relative fitness of the recipient population following a single translocation event, emphasizing the effect of the genomic architecture of preadaptive (PA) and maladaptive alleles (MA) on fitness. Fitness was a function of  $\Delta_{MA}$  (maximum possible fitness reduction in an individual carrying all maladaptive alleles),  $\Delta_{PA}$  (maximum possible fitness increase in an individual carrying all preadaptive alleles), and  $\Delta_{OD}$  (fitness reduction of a genotype heterozygous for all loci relative to local or foreign double homozygotes due to outbreeding depression) (gray dashed line, relative fitness of 1.0; colors, different numbers of outbreeding depression [OD] loci pairs; continuous and dashed lines, variable numbers of maladaptive alleles [MA]). Total immediate fitness effect of introduced individuals was held constant, and fitness contributions were  $1 + s$  per locus, where  $s$  is the selection coefficient per preadaptive and maladaptive locus. Unlike Figures 1, 3, and 4, the x-axis on this plot extends to generation 100.

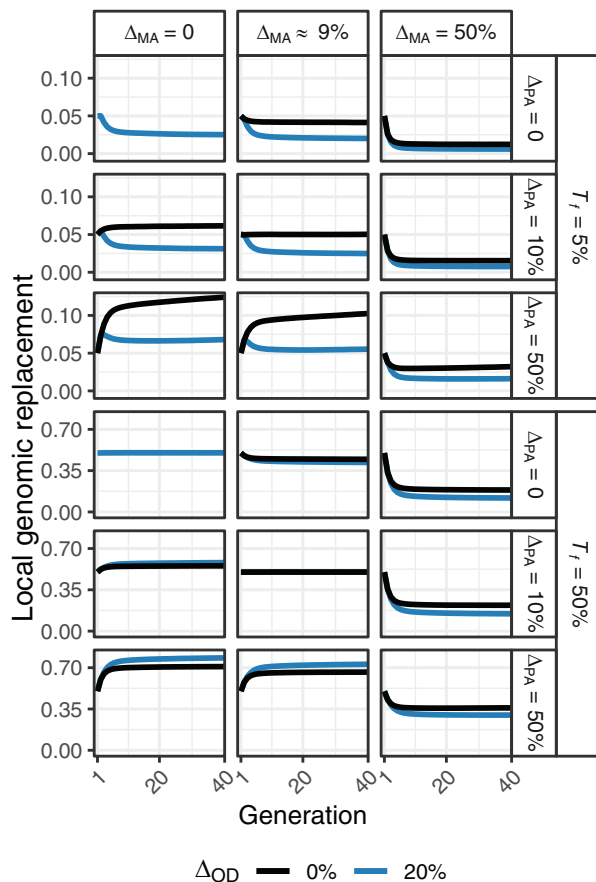
value within ~50 generations (Figure 2). However, fitness gains were much slower with genetic architectures that had more loci of weaker effect. In contrast to preadaptive alleles, the architecture of maladaptation and OD had relatively little effect on long-term population fitness when the translocation fraction was small (Figure 2 & Appendix S3). However, for a given strength of OD and  $\Delta_{MA}$ , mean fitness was slightly higher in cases with fewer OD pairs or maladaptive alleles with larger effects, even though the total strength of selection was equal regardless of the number of loci (Appendix S3).

One possible concern surrounding AGF is the replacement of native genetic variation in the recipient population. Local genomic replacement varied over time, but it was less than the fraction of individuals translocated ( $T_f$ ) when maladaptation was strong (Appendices S5 and S6). When maladaptation was comparatively weak ( $\Delta_{MA} < 10\%$ ), the strengths of OD, preadaptive, and maladaptive alleles determined whether LGR was  $> T_f$  (Figure 3 & Appendix S5).

The interaction of OD and adaptation was highly dependent on the proportion of translocated individuals. When translocating a modest number of individuals ( $T_f = 5\%$ , shown in Figure 3), local genomic replacement was highest when the effects of positive selection ( $\Delta_{PA}$ ) outweigh negative selection ( $\Delta_{MA}$  and  $\Delta_{OD}$ ) (Figure 3). Qualitatively similar results were obtained with a lower translocation fraction ( $T_f = 0.5\%$ ) and are

presented in Appendix S6. When the translocation fraction was very large ( $T_f = 50\%$ ), local genomic replacement exceeded the translocation fraction value when  $\Delta_{MA}$  was low and  $\Delta_{OD}$  was high, presumably because with 50% introduction, the OD loci were exactly at a fitness saddle and genetic hitchhiking from the PA alleles caused an increase in introduced OD alleles, leading to resolution of those loci toward introduced alleles. When selection strengths on preadaptive and maladaptive alleles exactly equaled each other ( $\Delta_{PA} = 10\%$  and  $\Delta_{MA} \approx 9.1\%$ , or both equal 0.0), a stable equilibrium was reached and LGR remained at 0.5 for all OD levels (Figure 3). These results were independent of dominance patterns of maladaptive loci and number of preadaptive, maladaptive, and OD loci (Appendices S1 and S7).

When translocation effort was divided among 5 pulses, fitness reduction was lower (e.g., relatively higher fitness) than when translocating all individuals in a single event (Figure 4a). In general, the architecture of loci contributing to OD (e.g., number of pairs of loci) had less of an impact on fitness and local genomic replacement than the overall strength of OD (Appendices S8 & S9). Additionally, with OD, LGR was lower in pulsed scenarios in the short term given fewer individuals were introduced at each event and the frequency of introductions (Figure 4b). Although pulsing sometimes marginally increased minimum fitness (Figure 4c), relative fitness remained low for a longer period of time in comparison with when all individuals



**FIGURE 3** Local genomic replacement fraction for the first 40 generations under a translocation fraction ( $T_f$ ) of 5% and 50% following a single translocation event in generation 1 ( $\Delta_{MA}$  is the maximum possible fitness reduction in an individual carrying all maladaptive alleles,  $\Delta_{PA}$  is the maximum possible fitness increase in an individual carrying all preadaptive alleles, and  $\Delta_{OD}$  is the fitness reduction of a genotype heterozygous for all loci relative to local or foreign double homozygotes due to outbreeding depression). Parameters are as in Figure 1. The y-axes differ between the 2  $T_f$  values.

are moved in a single event (Figure 4a & Appendix S8). After the short-term effects of pulsing subsided, both local genomic replacement and relative fitness values of single translocation or pulsed translocation events converged on the same values after approximately 30 generations (Figure 4a).

In the absence of OD, introducing foreign individuals over many generations in a pulsed manner did not offer any measurable benefit over translocating all individuals at once ( $\Delta_{OD} = 0\%$ ) (Figure 4c). However, in extreme cases of OD (e.g.,  $\Delta_{OD} = 60\%$ ), pulsing did mitigate some of the initial fitness reduction following translocation as compared with introducing individuals in a single event (Appendix S10). Overall, changing the frequency of translocation events—whether every 1, 2, or 4 generations—offered marginal decreases in overall population fitness reduction.

## DISCUSSION

AGF can be a useful and powerful tool for conservation and production management. However, in many cases the

advantages are small or take several generations to accrue, and the potential disadvantages of AGF caused by OD and the introduction of locally maladapted alleles may have short-term consequences that need to be overcome.

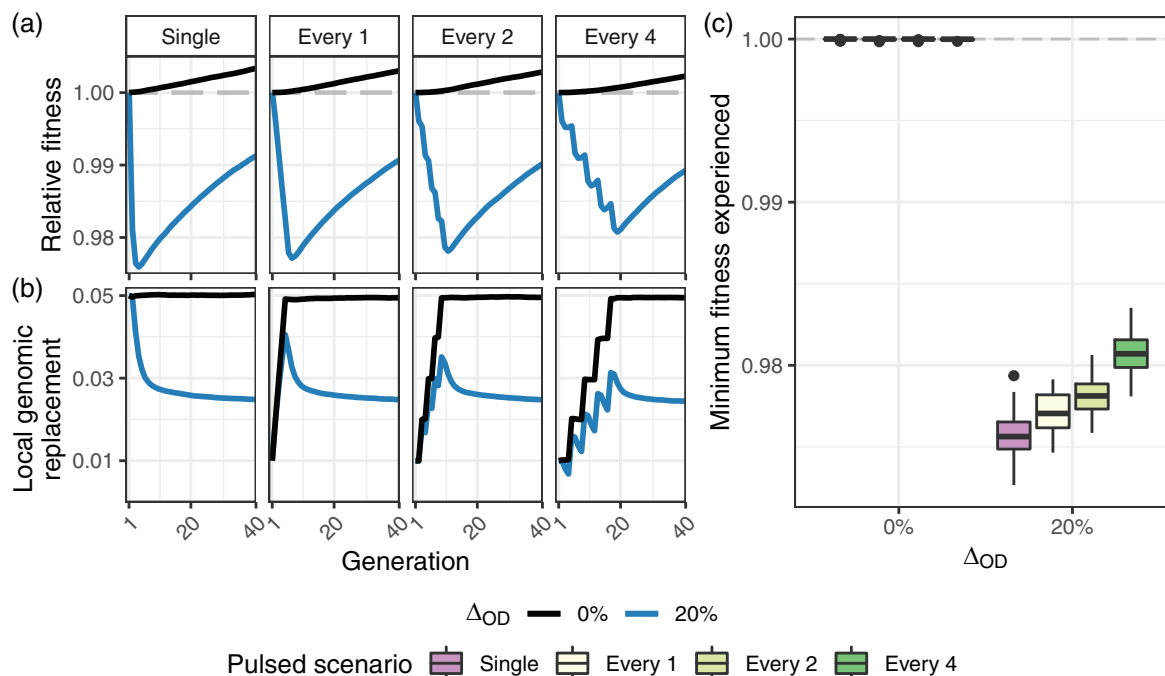
## Short-term increases in fitness

AGF in large populations, while sometimes causing a reduction in fitness immediately following translocation, often increases population-level fitness in the long term. However, even in most beneficial scenarios, AGF only provided strong benefits soon after translocation (e.g., within the first ~10 generations) when the introduced genotypes have a large fitness benefit caused by large-effect alleles. The exact fitness response resulted from a complex interplay between selection on loci with deleterious (maladaptive alleles and OD loci) and beneficial (preadaptive alleles) genetic variation and their genomic architectures. The number of individual migrants (translocation fraction) had a significant impact on both the fitness response and amount of recipient population genome replaced. Specifically, both positive and negative fitness effects were exaggerated with higher migration levels. When the translocation effort was divided into pulses across generations as opposed to a single translocation event, fitness reductions and genomic replacement were somewhat mitigated, but at the cost of further delayed benefits.

Our results indicated that the conservation outcomes of AGF may often be fairly modest in large populations. We assumed a rather extreme situation in which all fitness-affecting alleles were reciprocally fixed in donor and recipient populations. While extreme, reciprocal fixation displayed the maximum effect that AGF may have on population mean fitness. We predict that AGF's effects—both beneficial and harmful—will be dampened in situations where populations are more closely related and allele frequency differences are less extreme. Furthermore, when there were many preadapted loci of small effect, we found that population mean fitness had not appreciably increased even 40 generations after AGF (Figures 1 & 2; Appendix S3). The effects of AGF on population mean fitness in long-lived species, such as trees or corals, many of which have generation times in excess of decades (Babcock, 1991; Howe et al., 2006), may be too slow to help large populations cope with rapidly changing climates.

## Genomic architecture of adaptation

We examined fitness effects resulting from different genomic architectures of 3 types of loci: preadaptive alleles, maladaptive alleles, and those causing OD. Beyond modifying the number of these loci across the genome, we also varied their total effect to explore the potential positive and negative effects of AGF. One of our key findings was that the long-term fitness outcome of AGF was highly dependent upon the nature of the preadaptive alleles. Fitness gains were rapid when the selected trait was controlled by 1 or few loci of large effect. Conversely, when the trait was controlled by many loci of small effect, fitness gains were very slow and of limited benefit, even when the total possible



**FIGURE 4** (a) Relative fitness and (b) local genomic replacement by outbreeding depression level over the first 40 generations for each translocation scenario (i.e., single translocation versus 5 events of pulsed translocations every 1, 2, or 4 generations). The total number of individuals translocated is the same in each scenario (i.e., 500); each pulsed introduction was one-fifth the size of the single 1-time introduction). (c) Variation across 50 replicates of each translocation scenario with the same data as in (a) and (b). Results are for total migration rate of 5%, 5 preadaptive and maladaptive alleles with a  $\Delta_{PA} = 10\%$ ,  $\Delta_{MA} \approx 9.1\%$  (dominance coefficient of 0.5), and 10 pairs of outbreeding depression loci ( $\Delta_{MA}$  is the maximum possible fitness reduction in an individual carrying all maladaptive alleles,  $\Delta_{PA}$  is the maximum possible fitness increase in an individual carrying all preadaptive alleles, and  $\Delta_{OD}$  is the fitness reduction of a genotype heterozygous for all loci relative to local or foreign double homozygotes due to outbreeding depression).

benefit for preadaptive loci was the strongest (50 preadaptive loci and  $\Delta_{PA} = 50\%$ ) (Figure 2 & Appendix S3). A similar result was found when examining the effects of genetic architecture of heat tolerance in coral, where simulated populations went extinct more quickly and had higher reductions in population size when thermal tolerance was controlled by many loci (Bay et al., 2017).

It is important to understand the specific causes of fitness gains resulting from AGF, particularly in terms of a trait's genetic architecture. When translocating beneficial alleles only, an initial recipient population fitness increase results from the translocation itself because the population now includes individuals with novel beneficial alleles. Subsequent fitness gains following this initial fitness bump result from selection. The fitness change due to selection will be directly proportional to the magnitude of the selective effect on loci controlling the trait. Therefore, for the same maximal effect of preadaptive loci on the fitness of an introduced individual ( $\Delta_{PA}$ ), traits controlled by a few alleles of large effect will generate more additive genetic variance than traits controlled by many loci with small-effect alleles (see Appendix S11 for a derivation based on Fisher's fundamental theorem). As a result, traits controlled by large-effect alleles will contribute more to a population's adaptive potential.

AGF is not likely to confer practically relevant benefits within a few generations for large populations given that many traits are polygenic. Empirical studies have shown climate-related traits are often controlled by many small-effect loci (e.g., Fuller et al., 2020; Rose et al., 2018). For instance, drought toler-

ance in European populations of *Arabidopsis thaliana* is polygenic and associated with 151 single nucleotide polymorphisms (SNPs) (Exposito-Alonso et al., 2018). Similarly, tolerance to warm marine temperatures in *Acropora* corals is associated with variation at 114 SNPs (Bay & Palumbi, 2014). Although managers without genomic resources are at a disadvantage, it bears reminding that AGF rarely results in long-term fitness declines (Appendix S3). Thus, a rough estimate of a trait's genetic architecture or an estimation based on related species or similar traits may be helpful.

## Maintaining local genetic identity

One concern raised by AGF is the loss of local genetic identity in the recipient population due to genetic swamping from the donor population, a process we term local genomic replacement. Through the process of AGF, some fraction of the local genome will be derived from outside sources. In extreme cases, hybridization between donor and recipient populations could lead to the recipient population's genomic extinction and therefore the loss of its genetic integrity (Todesco et al., 2016). Maintaining such genetic integrity (e.g., Hauskeller, 2007) may be more important in some conditions (conservation) than others (optimizing resource extraction), but the case-by-case need for maintaining genetic integrity is a philosophical question beyond what we consider here (but see Rohwer & Marris [2015] for an in-depth treatment of this topic).



In the cases we simulated, the amount of local genomic replacement was largely a function of translocation fraction ( $T_f$ ). Under likely more realistic levels of translocation ( $T_f \leq 5\%$ ), the amount of local genomic replacement was typically less than the translocation fraction. However, this replacement of local genetic variation by translocated alleles was greatest when there were the greatest fitness benefits of AGF. The exceptions were combinations of weak total selection strength on maladaptive alleles ( $\Delta_{MA} < 10\%$ ) while selection was strong on preadaptive alleles ( $\Delta_{PA} = 50\%$  [Appendix S6]). When a large number of individuals was translocated ( $T_f = 50\%$ ), genomic turnover exceeded 80% in some cases (Appendix S6). In some real-world cases, such as reforestation of harvested sites following clearcutting, many millions of individuals representing a substantial fraction of the population may be replanted across a species range in a year. In British Columbia, for example, 259 million trees of various species were replanted in 2016 alone (<https://news.gov.bc.ca/factsheets/factsheet-reforestation-in-bc>).

### Pulsed translocation efforts

We examined whether dividing the translocation effort into discrete pulses, here represented as 20% of the total number of individuals to be moved in 5 separate events, had an effect on the recipient population's fitness response. Overall, in comparison with translocating all individuals in a single effort, pulsing alleviated some of the negative fitness effects resulting from AGF. In particular, translocating individuals every 4 generations resulted in lower fitness reductions (e.g., relatively higher fitness) compared with more frequent pulses or a single migration (Figure 4c), but this effect was modest with biologically realistic levels of OD.

Although populations showed reduced levels of both fitness reductions and local genomic replacement as a result of pulsing (Figure 4), they also experienced these depressed levels for a longer period. Similarly, although pulsing mitigated fitness reductions when OD was strong, it also delayed the fitness benefits of gene flow when introduced individuals had a high fitness (high  $\Delta_{PA}$ , low  $\Delta_{MA}$ ) and weak OD (low  $\Delta_{OD}$ ). Hence, although pulsing helped reduce fitness reductions in some scenarios, it also delayed fitness gains in others. On balance, with realistic parameters, the outcomes of AGF were improved by a single large pulse of translocation.

### Considerations for managers

We simulated a fitness increase of up to 50% resulting from preadaptive alleles, meaning that individuals from the donor population had 50% higher fitness in the new environment. Studies in natural populations show that the strength of local adaptation is of that order in a wide variety of species (Bontrager et al., 2020). Similarly, Exposito-Alonso et al. (2019) reported strong climate-mediated natural selection in *A. thaliana* from common garden transplants where >60% of populations were killed due to non-native conditions. However, estimating the beneficial effect of preadaptive alleles in a novel ecological and

genomic context is extremely difficult in natural settings. Furthermore, if an environment is predicted to change in a particular direction over time (e.g., trend of climatic warming), the selective benefits of preadaptive traits may increase in the future. In general, the benefits of preadaptive alleles from AGF may take many generations to realize in large populations (Figure 1 & Appendix S3), and an important consideration is whether long-term gains outweigh short-term fitness costs.

AGF has been proposed as part of a decision tree for managing coral reef restoration (Van Oppen et al., 2017). In such systems, our results can be used to guide management decisions, but we are aware that estimates for many of the parameters we simulated will not be available in most systems. It is therefore important to consider the results qualitatively and in relative terms. For instance, little is known about OD and its underlying genetic mechanisms in many systems. Our results show that OD should be a consideration only when it is extremely strong (e.g., between very divergent populations representative of interspecific crosses [Appendix S3]). Given that AGF is typically done with closely related populations, OD is not likely to play a strong role in reducing the benefits of AGF in large populations. Similarly, little is known about alleles originating in source populations that are deleterious in the recipient population. Our results highlight that  $\Delta_{MA}$  matters when it is strong (e.g., when fitness is reduced in an individual by >10%).

Based on our results, we generated some suggestions for managers considering AGF in large populations. First, performing controlled breeding trials before going all in at the population scale in the wild may be helpful. Many problems resulting from OD or maladaptive alleles could be screened by measuring growth and fitness in  $F_1$  (and  $F_2$  and beyond) individuals resulting from donor–recipient crosses. Indeed, using  $F_1$  individuals in AGF attempts may help reduce the fitness reduction the population may experience. Second, translocating fewer individuals at a time (i.e., a smaller translocation fraction) is one way to mitigate population-level harm if breeding trials are not able to occur before translocation and unforeseen risks manifest in reductions of individual-level fitness and fecundity. And last, if these options are not available, landscape genomic techniques that merge species distribution models with the knowledge of adaptive loci can generate recommendations for assisted migrations (Shryock et al., 2020).

In spite of a broad parameter space that we explored in our simulations, we did not examine all factors that might be considered while deciding to perform AGF. First, we did not model carrying capacity or a fluctuating population size. Second, we did not consider other consequences of translocations, such as disease and parasites or disruptions of social structures. Furthermore, even though adaptive genetic variation may help a population cope with environmental change, climatically induced range shifts may increase interspecific competition in certain contexts (Razgour et al., 2019), which is a factor we did not consider. Finally, introducing outside genotypes may enhance the population from the direct effects of including more fit genotypes, rather than through the effects on the future gene pool; movement of individuals may increase recipient population productivity within the same generation.

## Future work

Our study contributes to a deeper understanding of some of the genetic factors determining outcomes of AGF in large populations. Nonetheless, the results and parameter choices we made have exposed some avenues that future research should pursue. First, we assumed that beneficial (preadaptive) alleles were reciprocally fixed between donor and recipient populations. This is likely to be an oversimplification—it is possible that these preadaptive alleles may already be present at a low frequency in the recipient population. The change in additive genetic variance (and therefore fitness) is going to be less in situations for alleles that are introduced into a population where they are already present at a low frequency, as compared to changing an allele's frequency from 0% to ~5% (see the Supporting Information for further discussion). Exploring the cases with a translocation fraction ( $T_i$ ) of 0.5% may give an approximate representation of preadaptive alleles being present at a low frequency. In this case, however, preadaptive alleles will be in linkage disequilibrium (at least in the early generations following translocation), which might not be an accurate representation of these alleles existing at low frequencies in natural populations. On a related point, further research is necessary into the uncertainty of positive selection strength of preadaptive loci. We modeled a constant positive selection strength over time, but selection strength may increase in the future with a changing environment. In such cases, the benefits from AGF may be more frequent or stronger than our results imply.

As climate change intensifies and populations experience fitness reductions and extirpations, management strategies, such as AGF, will become a more widely considered tool for “prescriptive evolution” (Smith et al., 2014). Our results indicate that the conservation outcomes of AGF in large populations may be fairly modest in real-world settings. In our simulations, we assumed a rather extreme situation where all fitness-affecting alleles were reciprocally fixed in donor and recipient populations; this allowed us to determine the maximum effect that AGF may have on population mean fitness.

Although detailed knowledge of OD and the genetic architecture of adaptive (both pre- and maladaptive) traits would greatly improve predictions regarding the long-term success of AGF, such knowledge is often rudimentary at best and limited to model systems. However, tools such as controlled breeding trials or landscape genomics can help inform managers before conducting AGF. Although AGF in large populations often has limited short-term fitness consequences, its long-term benefits suggest it may be a useful management tool moving forward to help populations adapt to a changing climate.

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## ORCID

Jared A. Grummer  <https://orcid.org/0000-0003-3627-0769>  
 Tom R. Booker  <https://orcid.org/0000-0001-8403-6219>  
 Remi Matthey-Doret  <https://orcid.org/0000-0001-5614-5629>  
 Pirmin Nietlisbach  <https://orcid.org/0000-0002-6224-2246>  
 Andréa T. Thoma  <https://orcid.org/0000-0002-9755-2674>  
 Michael C. Whitlock  <https://orcid.org/0000-0002-0782-1843>

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