**Eco-evolutionary models of population decline: How and when can we use connectivity to support and restore populations on the brink of extirpation?**

Gina Lamka1 and Janna Willoughby1

1. College of Forestry, Wildlife, and the Environment, 602 Duncan Dr., Auburn University, Auburn, AL 36849

ABSTRACT

As we continue to lose biodiversity and convert green spaces to roadways and buildings, connectivity between populations will continue to decline. In threatened and endangered species, this is particularly concerning because the cessation of immigration bringing in new alleles into already small, isolated populations can tip populations into an extinction vortex. This, in turn, can cause increased inbreeding and further loss of genetic diversity, leading to lower adaptability and higher extirpation probabilities in these populations. To counter these trends, management actions such as assisted migration and the construction of corridors aim to increase genetic diversity and extend population viability. Unfortunately, monitoring genetic diversity change and predicting the extent of new genetic variation that is needed to prevent extirpation is difficult and costly *in situ*. Therefore, we designed an agent-based model to link population-wide genetic variability and the influx of unique alleles via immigration to population stability and extirpation outcomes. Using our model, we simulated vulnerable populations, namely populations with a stochastic drop in population size, decreased heterozygosity, and increased inbreeding, and instituted an extinction-vortex-like fitness parameter whereby individuals that were more genetically diverse were more fit than those with less genetic diversity. Using multiple model runs, we quantified the number of migrants carrying new alleles and the frequency of increased migration required to demographically restore these reduced populations. We also quantified how these parameters interact with each other and demographic variables relating to vulnerable populations. Finally, we considered how the restored populations genetically differ from populations that would have remained in those locations if habitat conditions had not caused a crash. Combined, these data illustrate how management of connectivity can be critical in restoring at-risk populations, but that these management actions have long-lasting effects on the genetic composition of these populations. Understanding how these at-risk populations change with management interventions has broad implications for the long-term adaptability of these populations and require further efforts for protecting locally adapted allele complexes when connectivity is restored.

INTRODUCTION

As habitat fragmentation continues to plague wild environments, connectivity between populations will remain a priority for population management. Threatened and endangered species are those that are of highest conservation concern and therefore require more immediate intervention due to already decreased levels of diversity and increased inbreeding in response to small population sizes. However, understanding diversity in wild populations requires an understanding of the ecology and evolutionary history of these populations. Traditionally, ecology examines the relations of organisms to each other and their physical environment, while evolution explores the diversity between generations via genetic diversity (Post and Palkovacs 2009). Utilizing both frameworks, understanding eco-evolutionary feedbacks can aid in recognizing mechanisms that drive individual and population level differences in fitness at the center of ecology and evolutionary interactions (Post and Palkovacs 2009). Gaining further understanding of these relationships will bring insight into how populations may respond to environmental change, and the management of ecosystems can gain direct advantages from a further understanding of the ways that populations evolve with the landscape.

Often, conservation biology is focused on a particular eco-evolutionary model, the extinction vortex. In this model, small populations are of high conservation concern because these populations are at the greatest risk of extirpation. Because these small populations are typically isolated, these populations may be susceptible to extirpation due to stochastic events, and they will often have reduced genetic diversity (Caughley 1994). Genetic diversity ultimately alters population stability via the extinction vortex when inbreeding depression (decline in average individual fitness due to mating of related individuals) and genetic drift (fluctuation of genetic variation over time due to random sampling) reduce genetic diversity and fitness in a feedback loop (Caughley 1994; John M. Drake et al. 2006; J. M. Drake 2008; Braumann 2010; Messer 2016). When genetic diversity is diminished and inbreeding increases, populations face increased expression of recessive traits, increased presence of unfavorable genes (genetic load), and decreases of gene diversity (Coltman and Slate 2003; Del Castillo et al. 2011).

In addition to the idea of an extinction vortex in small populations, eco-evolutionary patterns are also present in declining populations. This relationship is apparent when environmental changes shift the fitness landscape, and behaviors and life-history strategies of particular populations no longer result in sufficient offspring (Norris 2004). Importantly, it can be difficult to diagnose causes of population decline because causes are often limited to the specific population studied, as different factors may limit different populations and species (Blaustein and Kiesecker 2002; Peery et al. 2004). This means that alleviating these pressures on the population can be impossible because the root cause of decline remains unknown. In addition, small population size and declining population size often happen in tandem, meaning that the mechanism of either in isolation is difficult to disentangle, further adding to the confusion around the root cause.

Actions to increase the connectivity of populations are enacted by agencies responsible for management, such as the US Fish and Wildlife and state government biologists. Oftentimes, management practices have the goal of both increasing population size and genetic diversity by restoring gene flow and outbreeding with individuals that have alternate allele frequencies. Translocations, reintroductions, and assisted migrations all bring in an influx of new, unique alleles to introduce genetic variability in inbred populations. In some cases, introducing alleles that are not locally adapted has its own suite of difficulties in population management, such as outbreeding depression and high population divergence. Unfortunately, consistently monitoring the genetic diversity of wild populations – both vulnerable and otherwise – before and after management intervention is both costly and difficult *in situ*. Therefore, establishing simulation models that can monitor diversity across hundreds of years is fundamental in evaluating the cost-benefit of artificial introduction of genetic diversity.

To understand these long-term effects of migration, we developed an agent-based model that uses genetic diversity and gene flow to determine fitness in small populations. These modeled populations provide insight into how populations persist in the face of stochastic and anthropogenic ecosystem change. Specifically, we examined how dispersal can mitigate the effects of small populations and inbreeding, and the genetic implications of limited gene flow on these effects. Within our simulations, we examined trends following migration events to address three specific questions: 1. Do individual migrants’ genetic makeup influence genetic diversity change in recipient populations over long periods of time? We hypothesize that migrants with low fitness may result in more unstable populations long-term than migrants with higher fitness, since low fitness individuals may have reduced influence in the receiving population’s genetic pool, limiting the influx of new alleles passed on to future generations. 2. Does population size or trend alter the magnitude of the recipient population’s response to immigration over long periods of time? We hypothesized that extremely small populations will retain more of the migrant-related genetic variants than populations with more moderate population crashes due to the population growth potential in extremely small populations. 3. What are the relative magnitudes of individual-level vs. population-level influences on migration induced changes in the recipient population? Since small populations are influenced more by evolutionary forces, adding migrants can buffer against genetic erosion to a greater degree when population crashes are greatest. We considered the effects of changes on the number of individuals in the population, the genetic diversity within the population, the divergence from the original and source populations over time, and the reproductive success of individuals following immigration events as well as the proportion of simulated populations that persisted after migration ceased. These aims will support future considerations of promoting migration (via corridors or translocations) when managing species on the brink of extinction.

METHODS

To identify the long-term impacts of migrants on a struggling population, we developed a forward-time agent-based model that tracks individuals and their multi-locus genotypes for 350 years. Parameters were selected and evaluated separately to examine their independent and interaction effects on the simulation (Param Table 1). We modeled migration by creating two populations: the focal population in which the simulation was enacted and a source population so that migrants could be randomly selected to disperse unidirectionally from the source population into the focal population. In all simulation runs, the focal population stabilized for 100 years, went through a quick (10 year) population decline to simulate stochastic environmental change, persisted at the low population size for 40 years to simulate various IUCN and state agency management classifications (vulnerable, KB = 700; threatened, KB = 500; endangered, KB = 300; critically endangered, KB = 100; Param Table 1), and then allowed the population to grow again to the original carrying capacity (k = 1000) to simulate successful habitat restoration management for an additional 200 years. The basic model structure is described in text and details are in Supporting Information.

Simulations began by initializing the populations so that the focal and source populations were at carrying capacity (total population size focal, k = 1000, total population size source, s = 5000) and all individuals were assigned genotypes with 1100 SNPs. Single nucleotide polymorphisms were split into two types; 1000 SNPs (nSNPD) were randomized as either homozygous or heterozygous according to the defined minimum allele frequency (0.05 ≤ p ≤ 0.15 or 0.40 ≤ p ≤ 0.50; Param Table 1) and 100 SNPs (nSNPM) were population specific such that the focal population was homozygous for one allele and the source population was homozygous for the alternative allele. Loci were used to characterize the changes in genetic diversity in the population associated with immigration. Heterozygosities over the randomized SNPs and across all SNPs were calculated at the individual level. For the initialized populations, sex and age were randomly assigned and all individuals were given a unique identification number.

The simulations began with ageing the population by one year. After ageing, individuals at the age of maturity were faced with fitness induced death in which there is a higher chance of mortality with decreasing heterozygosity. We then allowed randomized migrants from the source population to enter the focal population to examine how the influx of new alleles would alter the long-term viability. Migrants were permitted to enter the population at various frequencies to simulate constant connectivity (m = 1 migrant per generation), various assisted migration rates to simulate common management strategies (m = 100 individuals once, m = 25 individuals four times), or the absence of population connectivity (m = 0; Param Table 1). We classified assisted migration timings as either during the low population size, when habitat is still being restored (between years 110 – 150) and after habitat restoration when the population is permitted to grow again (year 151+; Param Table 1) to determine if bringing in new individuals before habitat quality is restored would have the same effect on the genetic diversity of the population as bringing new individuals after habitat management occurs.

After the migrants entered the population, random mate choice occurred so that migrants were permitted to breed but were not preferentially chosen so that the number of migrants did not equal the number of effective migrants. In one set of simulation runs, we preferentially chose migrants to examine how selection on migrants would influence the effect of migration events, which is described further in the Supplemental Instruction. Because we know that as population sizes decrease, there is a decreased chance of potential mates interacting with each other, we introduced an allee effect such that as the population size decreased, the chance of potential random mates meeting decreased. Mated pairs were given a random fecundity (0, 1, 2; Param Table 2) so that the total number of babies that were born allowed the population to grow along the logistic growth curve. Logistic growth was calculated with the equation

(1)

where the population size was determined by the per capita growth rate (*r* = 1; Param Table 2), carrying capacity (k = 1000), and the population size prior to reproduction (*Nt*). Additional babies were created to bring the population to the expected size and offspring genotypes were assigned according to Mendelian genetics where both the mother and father passed on 50% of their alleles to the next generation. Each SNP had a 0.1% chance of mutating (µ = 0.001) which is similar to empirical estimates of mutation in banner-tailed kangaroo rats (µ = 0.0081 mutants/generation/locus; Busch et al. 2007). The heterozygosity across all SNPs, the proportion of population-specific SNPs that have migrant ancestry, and the number of effective moms and dads were calculated to monitor the population. Finally, a density independent mortality event occurred so that there will be an increased chance of dying with increasing age, and all individuals over the maximum age of the species would die (Param Table 2). These life history events repeated in a loop for a total of 350 generations.

The population was monitored each generation with many population genetic measures. Along with the number of effective migrants and the number of effective parents, we also monitored population demographics such as the number of total individuals, the sex ratio, and the number of adults in each year. The number of migrants in the population and the proportion of migrant specific alleles in the population served as a way to determine how the influx of new individuals affected the focal population’s genetic diversity. Observed and expected heterozygosities across all SNPs served as the measure of overall individual and population wide genetic diversity. To examine how immigration of migrants into the focal population and random genetic drift changed the trajectory of the population, we calculated the amount of inbreeding in the population (FIS) and the amount of divergence in the focal population (FST) in that year as compared to the source population and compared to the initialized focal population (hierfstat package in R). Finally, the lifetime and relative reproductive success of all individuals was calculated by evaluating the number of mates, number of offspring, and the number of offspring that survived to maturity for all individuals. All figures and calculations were performed in RStudio (R version XX).

SI METHODS

Initialize focal and source populations  
Simulations began with the focal population at carrying capacity (k = 1000) and a large source population (s = 5000). Individuals were assigned an individualized ID number, age according to a Poisson distribution (rpois function) minus one, and a random sex (0 = female, 1 = male). Additionally, all individuals were characterized by two sets of SNPs: neutral and assigned with varying minor allele frequencies (nSNPD = 1000; 0.05 ≤ p ≤ 0.15 or 0.40 ≤ p ≤ 0.50) and fixed for different alleles in each population (nSNPM = 100) so that the focal population was homozygous for one allele and the source population was homozygous for the alternative allele. These different groups of SNPs were used to disentangle the effects of drift (nSNPD) and migration (nSNPM) across the genome. Therefore, a total of 2200 alleles describe each individual, with each locus defined as heterozygous with a code of 01 and homozygous with either 00 or 11. Relative fitness, calculated as the observed heterozygosity across the nSNPD loci was calculated for all individuals. The population then went through typical life history stages in a loop so that all life history events occurred at each timestep for a total of 350 years.

Loop for each timestep  
Age Up  
The first step in the model involved incrementing the age of all surviving individuals by one year. *Notice that because this is the first step in the model, the initialized population consisted of individuals that would be “born” in the first year.*

Death  
There were two functions that removed individuals from the population. Following the aging of individuals, a fitness-induced chance of death was imposed on the individual at the age of maturity equal to the inverse of the observed heterozygosity of the individual so that individuals with a greater heterozygosity had a greater fitness and a decreased chance of death. Additionally, as the last step in each simulation year, we assumed the cumulative probability of death of an individual was equal to the quotient of an individual’s age and the maximum lifespan. Individuals that were forced into mortality were removed from subsequent model steps. To reduce computational time, every 25 years, dead individuals were removed from the population object and written to another file that will be read back in before reproductive success calculations.

Migrate  
Migrants were randomly selected from the source population to move into the focal population, with the number and timing of migrants per generation selected determined based on the parameter set (Param Table 1). Although migrants move into the focal population, they are not preferentially chosen for mating pairs, so the number of migrants in the population are not equal to the number of effective migrants in that generation.

Mate Choice  
Reproduction occurred between randomly selected pairs of adults. Parents of the opposite sex were matched as mates with replacement so that individuals could mate with more than one individual in that year. An allee effect was imposed so that as the number of individuals in the population decreased, the chance of mates interacting decreased.

Pop Size Next  
The number of offspring produced per year was determined using the logistic growth equation so that the total number of individuals in the next year was calculated. The focal population was allowed to persist around carrying capacity for the first 100 years. Following that 100 year period, the population was forced through a bottleneck for 10 years, persisted at a lower carrying capacity for 40 years, and then allowed to expand at a rate of logistic growth until reaching the habitat’s original carrying capacity of 1000 individuals. Logistic growth was calculated with the equation

(1)

where the population size was determined by the per capita growth rate (*r* = 1), carrying capacity (k = 1000), and the population size prior to reproduction (*Nt*). The size of the carrying capacity at the duration of the bottleneck (KB) was quantified so that the new carrying capacity would be within limits for IUCN criteria for the evaluation for the Red List. Specifically, IUCN criteria evaluate species that are vulnerable as those that have > 10% decline in 10 years (KB = 700), endangered with a 50-70% decline in 10 years (KB = 300), and critically endangered with a 80-90% decline in 10 years (KB = 100). We defined a fourth intermediate category as threatened when the population had a > 10% and ≤ 50% decline in 10 years (KB = 500).

Breed  
Offspring genotypes were assigned according to Mendelian inheritance, where one allele at each locus was randomly selected from each parent. Mutation on generated genotypes was at a rate of 0.001 mutant/generation/locus. If an allele was selected to mutate, the allele was switched from either a 0->1 or 1->0 depending on the initial identity.

Lifetime Reproductive Success  
Prior to migration of source individuals into the focal population, we assumed there was no prior history of reproductive success for migrants. Therefore, at the conclusion of each replicate of the simulation, lifetime reproductive success was calculated by determining the sum of offspring that were generated by each parent.

Analyze  
After each generation, we calculated population demographics to monitor the population. Demographic calculations included the number of effective migrants, the number of effective parents, total number of individuals, the sex ratio, and the number of adults. The number of migrants in the population and the proportion of migrant SNPs (nSNPD) allowed us to monitor how migrant alleles were distributed across individuals. Genetic diversity and fitness were classified as the observed heterozygosity, calculated across all SNPs (nSNPD + nSNPM). Inbreeding in the population (FIS) and the amount of divergence in the focal population (FST) at that year as compared to the source population and compared to the initialized focal population were evaluated using the hierfstat package in R. After all simulation years, all dead individuals were written back into the population to calculate the lifetime (LRS) and relative reproductive success (RRS) of all individuals by evaluating the number of mates, number of offspring, and the number of offspring that survived to maturity for all individuals.

Sensitivity  
We compared the effect of all parameters on genetic diversity and population persistence by comparing the output of the simulated populations to control simulations. For each parameter set, we measured the heterozygosity and the distribution of each SNP type to examine how migration altered the genetic diversity of the focal population. Additionally, we evaluated pairwise FST values each year compared to the initialized populations. We ran 100 replicates for each combination of parameters, with each simulation run in R on a high-performance computing cluster (Easley).

*Model calibration with empirical data*

*While all parameter values are selected to simulate natural populations, input values and parameters need to be adjusted and calibrated to accurately reflect real-life scenarios. With that in mind, we compared the simulations to two known populations: banner-tailed kangaroo rats restricted to a 1 km area in southeastern Arizona and moose on Isle Royale. These two wild populations were selected with a matched-pairs concept in mind, so that the two species are similar in several life history traits (restricted in area and access to limited corridors between populations; are diploid, sexually reproducing mammals; are herbivores; reach maturity at 1 year old; and are solitary animals) but vary in generation time. As such, simulations will be compared to empirical data to correctly calibrate simulation parameters, and values will be altered to maintain a more accurate representation of wild populations.*

Table 1. Variable simulation parameters.

|  |  |  |  |
| --- | --- | --- | --- |
| Starting minor allele frequency | Migration rates | Low population size carrying capacitya | Year of migrations |
| 0.05 - 0.15 | 1 migrant per generation | Vulnerable k = 700 | Every generation |
| 0.40 – 0.50 | 100 individuals once | Threatened k = 500 | After habitat restoration 100@151; 25@151, 165, 181, 195 |
|  | 25 individuals four times | Endangered k = 300 | During habitat restoration 100@125, 25@125, 140, 155, 170 |
|  | No connectivity | Critically Endangered k = 100 | Every generation after restoration 1mig/gen@151 |

anote that the population size was below carrying capacity due to allee effects and mortality events

Table 2. Simulation constants for all runs.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Starting carrying capacity, focal pop (k) | Starting carrying capacity, source pop (k) | Number of randomized SNPs | Number of population specific SNPs | Maximum age | Maximum fecundity | Age of maturity | Total years | Population growth rate (r0) | Number of years for population decline | Duration of years at small pop size |
| 1000 | 5000 | 1000 | 100 | 9 | 2 | 1 | 350 | 1 | 10 | 40 |

RESULTS

The heterozygosity of the focal population remained largely unchanged following the stochastic population decline in connected populations, however there was an approximately 20% decline in heterozygosity following the stochastic population decline in a population without immigration, with little further change as the population size increased (Figure 2). In populations where there was no population connectivity until habitat was restored, management intervention increased the genetic diversity in the focal population more than if there was no assisted gene flow (Figure 3). Adding 100 individuals into the population increased genetic diversity quickly, but steadily declined to below the ideal one migrant per generation level after the 350 year period (Figure 3A). Surprisingly, adding 25 individuals in four migration events did not have the same effect as adding the same number of individuals at once, with the overall heterozygosity slowly decreasing after translocation events (Figure 3B). When simulating adding a corridor so that one migrant per generation could enter the population, the population’s heterozygosity increased incrementally over time, suggesting additional adaptive potential in this population (Figure 3C).

The timing of translocation events resulted in a slightly higher increase in overall heterozygosity in the immediate years following translocations when introduced when the population size is small, with the long-term trajectory of such changes being largely the same (Figure 4).

When two populations have similarly high starting genetic diversity, the heterozygosity will remain high when the populations are connected (Figure 5A). When the focal population’s starting genetic diversity is low, the heterozygosity will increase with migration events, with a greater increase in heterozygosity when the source population’s starting diversity is high (Figure 5A). However, having unconnected populations with high starting genetic diversity will have approximately 40% greater heterozygosity over time than having two connected populations that have low starting genetic diversity. In the same situations, the focal and source populations will diverge slower in highly diverse populations whether connected or not than in a focal population with low genetic diversity; a lowly diverse focal population will have a 2-fold and 3-fold higher FST when the source population has a low and high starting genetic diversity, respectively (Figure 5B).

Adding migrants into the population resulted in increased proportion of migrant alleles, resulting in approximately 40% migrant ancestry in constantly connected populations, 30% migrant ancestry when introducing 100 individuals once, and 20-30% migrant ancestry when introducing 25 individuals four times and when restoring the habitat with a corridor (Figure 6). In all cases, random genetic drift resulted in increased FST of the focal population as compared to the founding initialized focal population in a similar rate among migration rates, but with a greater effect when the stochastic population decline is greater (Figure 7A). Divergence from the source population increased when there was no migration, but the populations became more similar, and FST decreased, when migration occurred. The FST compared to the source population increased by approximately 50% when populations were not connected and decreased by approximately 50% when connected with one migrant per generation, with assisted migrations resulting in measures between these two ranges of FST (Figure 7B).

The average lifetime and relative reproductive success of the population was similar (LRS = 1.4) when the population size was stable but decreased as the population decreased and then increased when the population increased. As the population goes through a greater decrease in population size, the lifetime reproductive success of the individuals in the population must be greater to result in a population with the same carrying capacity (i.e., the maximum LRS = 2 in a vulnerable population but maximum LRS = 2.5 in an endangered population with the population is increasing; Figure 8).

*Additional things that my model can do that I didn’t do here (can implement in epiABM if desired):  
Preferentially choose migrants as mates – put in SI of this paper maybe?  
Parents have a higher chance of breeding with higher combined heterozygosity (natural selection)  
Enact higher fitness consequences when population density is low  
Have conserved (coding) SNPs in both populations that if get a mutation, can be lethal  
Instead of random migrants, select migrants based on heterozygosity [or something else]*

*SI FIGURES/RESULTS TO MAKE  
All the same figs, but in the other IUCN categories  
Ne vs Nc measures?  
migrant vs nonmig LRS – need to figure out how to define how many generations removed from a migrant parent is considered a “migrant” or “native” for this calculation*

Figures & Results

As the population went through stochastic population decline, changes in genetic diversity and divergence became more pronounced than when carrying capacity remained stable. In all simulation runs, the census population size declined to at or below the level as described in conservation rank designations due to allele effects and random death (i.e., when k = 1000, Nc ≅ 750; Figure 1A). Populations with greater declines in size resulted in greater changes in genetic diversity and population demographics. In most cases, populations were able to reach pre-bottleneck population sizes following habitat restoration; only when the population was critically endangered in the absence of migration did the population go locally extinct (13/100 simulation runs; Supplementary Figure 1). This cutoff for population extinction is an artifact of the limit of population persistence defined in the model (i.e., a population is locally extinct when there are less than 20 individuals in the population) and as such could result in a higher frequency of population crashes with more stringent limits on minimum population size (e.g., a limit of 50 individuals in the population). A picture containing diagram, text, line, plot

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Figure 1. Change in population demography measures in populations of various conservation rankings over time. (A) Census population size. (B) Proportion of migrant derived SNPs. Observed heterozygosity of putatively neutral SNPs (C) in the absence of migration and (D) when connected with one migrant per generation. Fst as compared to the initialized focal population (E) without and (F) with migration. Fst as compared to the initialized source population (G) without and (H) with migration.

Across conservation rank categories, observed heterozygosity increased over time both in connected and non-migrant connected populations, except for a short decline as the population dropped (year 150) at the endangered and critically endangered level (Figures 1C, 1D). Connected populations resulted in overall greater genetic diversity than in the absence of migration. When there was connectivity and one migrant per generation entered the population, the proportion of SNPs with migrant ancestry increased as the population declined, and continued to increase over time; threatened and vulnerable populations resulted in similar migrant ancestry, with nearly 100% migrant SNPs in the critically endangered population at the end of the simulation run (Figure 1B). Population divergence (Fst) trends were similar in the absence of migration and when compared to the original initialized focal population in a connected population; divergence increased over time with critically endangered populations resulting in the greatest divergence, followed by endangered, and was similar in threatened and vulnerable populations (Figures 1E, 1F, 1G). However, connected populations resulted in a decrease in Fst over time when compared to the migrant source population, as migrants immigrating into the population made the source and focal populations more similar (Figure 1H). At the end of the simulation (year 350), Fst ranged from 0.06 – 0.12 when compared to the migrant source population and 0.21-0.34 compared to the original focal population when they are connected with one migrant per generation.

The following results are reported for simulations of endangered species (drop from a carrying capacity of 1000 individuals to 300 individuals; see Supplemental Instruction for results from additional species status classification levels).

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Figure 2. Change in population demography with assisted migration strategies over time. (A) Proportion of alleles with migrant ancestry. (B) Observed heterozygosity of putatively neutral SNPs. (C) Fst as compared to the initialized focal population. (D) Fst as compared to the initialized source population.

The proportion of migrant SNPs increased drastically with assisted migrations, though connected populations resulted in a greater overall proportion of alleles with migrant ancestry in all generations (Figure 2A). As individuals were introduced and the population increased to its historical size, alleles with migrant ancestry was maintained over time, with the bulk introduction of 100 individuals resulting in 24% more migrant ancestry than repeated introductions (59% vs 36% migrant ancestry at year 200). Similarly, migrant ancestry was detected in connected populations as early as year 1, and continued to increase over time. The absence of migration resulted in no alleles with migrant ancestry in the population.

Observed heterozygosity increased over time in all cases except when the population crashed (year 150; Figure 2B). Both assisted migrations resulted in similar heterozygosities across all time points, resulting in greater genetic diversity than connected populations after the population reached its historical size (year 200). In the absence of migration, observed heterozygosity was lower than all populations with migrations, until year 350 when the connected population was similar in genetic diversity as those without any migrants.

Overall, trends for the divergence of the focal population from the original, initialized population was inversely related to the divergence of the focal population from the migrant source population. In all cases, Fst as compared to the historical, initialized population increased as the generation time increased (Figure 2C). As the population returned to its historical size, high frequency assisted migrations resulted in a similar Fst as populations without migrants. A bulk migration of 100 individuals diverged quicker than high frequency migrations, and connected populations resulted in even higher divergence to the original population. Similar to the original population, Fst of the focal population as compared to the migrant population increased in the absence of migrants (Figure 2D). However, migrants reduced the population divergence between focal and source populations, until migrants stopped being introduced in assisted migrations and Fst began to increase again. Connected populations are expected to continue to become similar to the migrant source population over time.

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Figure 3. Change in population demography with various starting allele frequencies (pH = 0.4, pL = 0.05) over time in connected and unconnected populations. (A) Proportion of migrant SNPs. (B) Observed heterozygosity. (C) Fst vs the initialized focal population. (D) Fst vs the initialized source population.

Whether the focal and source populations started with either a high or low starting allele frequency had no effect on the rate of migrant ancestry being represented in the population when one migrant per generation entered the population (Figure 3A). In the absence of migration, the observed heterozygosity increased slowly when starting allele frequency was low (t350 -t50 = +7%) and decreased at a similar rate when starting allele frequency was high (t350 -t50 = -7%; Figure 3B). Connected populations followed a similar trend when both populations had low starting allele frequencies, though being connected resulted in an overall higher heterozygosity than in the absence of gene flow. If two connected populations have high starting allele frequencies, the observed heterozygosity will be maintained at approximately the same level over time. The greatest difference in heterozygosity is when migrants contain higher diversity than the focal population, which results in a 17% increase in heterozygosity with an influx of new, diverse alleles (Figure 3B).

Divergence (Fst) from the starting focal population is slowest when both populations have high starting allele frequencies, and the absence of migration reduces the rate of divergence compared to connected populations (Figure 3C). When migrants have higher genetic diversity than the receiving population, divergence from the original population is greater than when both populations are low. Surprisingly, having high starting allele frequencies in connected populations results in similar divergence from the original population as having no migrants in a population that starts with low allele frequencies.

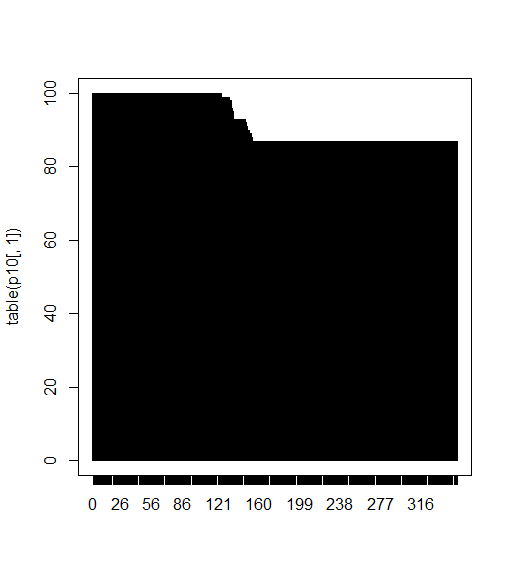
Divergence from the source population was greatest when both have low starting allele frequencies, especially without migrants bringing in alleles unique to the source population (Figure 3D). Divergence from the source population increased when there were no migrants and the starting allele frequencies were similar (i.e., both high or both low) and decreased in all other cases. When populations are connected and the starting allele frequency in the source population is high, the focal population becomes very similar to the source population (Figure 3D).

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Figure 4. Change in population demography responses to the timing of immigration events. Immigration could occur while the population is crashing (hot pink, lime green, royal blue) or while at the lowest population size (light pink, light green, light blue). (A) proportion of migrant SNPs (B) observed heterozygosity (C) Fst (D) Fst vs source population.

The timing that immigration events occur is important when monitoring the genetic diversity of the population. The greatest difference in population demography measures is when there are repeated migrations of a few individuals; reestablishing a corridor after a bottleneck event will have similar demographic characteristics to a fully connected population over a longer time, and bulk translocations respond similarly if the immigration happens during the crash as when it is at the low population size. Frequent assisted migrations during the population decline resulted in almost double the frequency of migrant alleles than if the translocations occurred after the population declined completely (Figure 4A). Because the proportion of migrant alleles was so different, the divergence from the source population reflected a similar pattern since those with more migrant alleles more closely resemble the source population (Figure 4D).



Supplementary Figure 1. Proportion of simulation runs that reached completion in the absence of migration when the population was critically endangered. All other simulations resulted in 100% completion.

DISCUSSION

Although one migrant per generation is regarded as the “ideal” population connectivity scenario, increasing fragmentation of populations limits this in reality. Here, we model different management strategies and evaluate how the 1) number and frequency of immigrants, 2) severity of the population crash, and 3) starting genetic diversities of the source and focal populations affect the long term viability and evolutionary potential of the population. We model scenarios where assisted migrations can serve as effective strategies for population management , and how establishing corridors or other connectivity strategies for consistent gene flow leads to better population sustainability than having no gene flow between poulations. Here, we further add to the large body of evidence that supports habitat restoration as the most effective strategy of population management and give a simulation model that can evaluate the risks and benefits of alternative strategies.

Similar to other theoretical and empirical research on the severity of population crashes to population viability, we show that populations that reach the threshold for a critically endangered classification status is at the greatest risk of extirpation. Indeed, in our system, critically endangered populations can die out within 24-54 generations after the start of a sharp population decline without the influx of new alleles via immigration. Further, we support previous work that identifies low heterozygosity, high divergence from locally adapted alleles, and high relatedness to migrant populations results in population with high intensity crashes (cite) and is further exacerbated without migration.

Predicting whether having one migrant per generation versus artificially adding immigrants into the population will result in greater population viability depends on the system and goal of management interventions. For example, gene flow can constrain adaptation to local conditions by passing on migrant derived traits, potentially lowering fitness via outbreeding depression. Accumulation of migrant derived traits over locally adapted traits occurs at a faster rate with consistent immigration as compared to bulk or low frequency assisted migrations and can result in lower genetic diversity. However, logistical limitations (e.g., time, investment, labor intensity, land management practices) will ultimately determine the management practice that is applied.

Investigation whether genetic diversity is related to conservation status is still outstanding (cite Janna’s IUCN paper, theta paper). Nonetheless, our simulations show that migrants that are highly heterozygous keep populations highly heterozygous as compared to populations with a low starting allele frequency or in the absence of migration. Although the adoption of migrant derived alleles is the same, the divergence to the original population is greatest when the focal population has a low starting allele frequency and divergence to the migrant population is smallest when migrants have high starting allele frequencies.

Theoretically, connectivity of subpopulations via one migrant per generation is sufficient to retain genetic variation while allowing divergence in allele frequencies; empirically, however, the minimum of one individual per generation is often insufficient to achieve neutral or positive population growth for struggling populations (Mills and Allendorf 1996). As such, the genetic connectivity of passing alleles via immigration must also be reflected via demographic connectivity so that the benefits of migrants are reflected in population growth and stability, a goal especially important for management of fragmented and threatened species (Lowe and Allendorf 2010). The benefits of migration – either naturally or via artificial translocations of individuals from one area to another – depend on the carrying capacity of the source and recipient populations, the rate of migration, the growth rate of the recipient population, and the frequency of repeated migration such that the outcome of immigration events are dependent on examination of these factors before using translocations as a conservation tool (Thrimawithana et al. 2013).

Just as small populations are at risk of extirpation due to the increased effect of individual genotypes, the benefits of management strategies in small populations are increased.   
 - small populations with an influx of high fitness indv benefits the population more  
 - the longer the population is small, the more pronounced the effects are  
 - is there a case study that mentions how there is a better establishment rate in low pop sizes?  
 - previous paragraph mentions outbreeding, maybe further develop these thoughts

The cost of management strategies that require assisted migrations is not limited to risks in genetic diversity and population stability, but also contributes to more time and resources that population managers must devote to sustaining the species.   
 - find citation about the cost of either one time or consistent introductions  
 - mention the proportion of funds that go to T&E species?  
 - can you find anything about the number of people required for such an effort?

Wildlife agencies are forced to examine management strategies in a cost-benefit analysis. Here, we establish a strategy to examine if implementing changes in migration among populations is better than letting the population evolve on its own. In some cases, allowing the population to persist in the face of stochastic change rather than introducing new alleles is effective enough for population sustainability due to the longstanding evolutionary potential that has been built up and progressed over time. This is especially true depending on the starting genetic diversity of the two populations and if the migrants have locally adapted alleles that are important for fitness. Although we touch on how differing traits from different populations can be altered with migration, future work on selection of desired traits and local adaptation effects is necessary.

Migrants typically have lower fitness than the population (Buchan et al. 2019), perhaps to avoid unfavorable conditions in the source population. That is not always the case, however, as individuals that are bold are more likely to travel to new territories (Chapman et al. 2011), and boldness can lead to higher reproductive success (and therefore, fitness; Reale et al. 2009; Gasparini et al. 2019). Despite this understanding of the proximate effects of migration on individuals fitness and population stability, how long these effects persist in recipient populations was previously unclear. For example, it is possible that immigrants provide a temporary boost in genetic diversity to small, inbred populations but that many of these new alleles, which may not be beneficial in the local environment, are lost from the population in a few generations. Alternatively, the influx of new alleles may persist in the new populations, particularly when small populations grow quickly, providing a lasting pool of genetic variants. Utilizing simulation models like we present here allows population managers to examine the range of potential effects of gene flow in their species of interest.

Conclude with some remarks about how many of these problems would be alleviated with increased habitat quality and decreased fragmentation.  
 - corridors are an effective strategy that boosts habitat quality and increases viability  
 - passive movement of the pops are better than active assisted migrations  
 - do corridors increase the amount of public interaction with nature? Mention some benefits to humans of having corridors.

**Lit to keep in mind**

**Equations/other**

[Effects of metapopulation processes on measures of genetic diversity (royalsocietypublishing.org)](https://royalsocietypublishing.org/doi/epdf/10.1098/rstb.2000.0740) – has some equations that might be helpful – looks at different ways gene diversity changes with migration

[Application of the One‐Migrant‐per‐Generation Rule to Conservation and Management (wiley.com)](https://conbio.onlinelibrary.wiley.com/doi/pdfdirect/10.1111/j.1523-1739.2004.00440.x) – Wang 2004 evaluates the one migrant rule. Lots of equations and such here.

[EconStor: The complexities of agent-based modeling output analysis](https://www.econstor.eu/handle/10419/230635) – talks about how to analyze and report ABM outcomes.. including “issues surrounding variance stability (in connection with determination of appropriate number of runs and hypothesis testing), sensitivity analysis, spatio-temporal analysis, visualization, and effective communication of all these to non-technical audiences, such as various stakeholders”

**Empirical case studies**

[Temporal dynamics of migration‐linked genetic variation are driven by streamflows and riverscape permeability - Kelson - 2020 - Molecular Ecology - Wiley Online Library](https://onlinelibrary.wiley.com/doi/full/10.1111/mec.15367) – this is an empirical study that followed genetic diversity in a salmonid across different stream permeability scenarios (i.e., restricted or unrestricted migration) – may be good for a case study in discussion?

[A single migrant enhances the genetic diversity of an inbred puma population | Royal Society Open Science (royalsocietypublishing.org)](https://royalsocietypublishing.org/doi/full/10.1098/rsos.170115) – GREAT case study – ONE puma crossed a road, had 11 offspring, and influenced the pops inbreeding and genetic diversity measures

[Exploiting genetic diversity to balance conservation and harvest of migratory salmon (cdnsciencepub.com)](https://cdnsciencepub.com/doi/full/10.1139/cjfas-2012-0449) - (genetic data from 38 single nucleotide polymorphisms, assayed in 96 populations) to detect migratory trends in stock composition of sockeye salmon returning to Bristol Bay and to inform fisheries management in real time.

**simulations**

[The Society for Conservation Biology (wiley.com)](https://conbio.onlinelibrary.wiley.com/doi/epdf/10.1111/j.1523-1739.1987.tb00023.x) – Lacy 1987 – simulation with the conclusion that genetic drift is strong in pops and connectivity via migrants can counter the strong effect of drift.

[Modelling the consequences of duck migration patterns on the genetic diversity of aquatic organisms: a first step towards a predictive tool for wetland management - ScienceDirect](https://www.sciencedirect.com/science/article/pii/S1146609X02011517#FIG1) – simulated duck migration and looked at gene frequencies changes based on the landing sites on ducks – “The modelling framework is designed to develop hypotheses on the likely impact of duck migration on genetic diversity of aquatic organisms”.

[Effect of migration and environmental heterogeneity on the maintenance of quantitative genetic variation: a simulation study - McDonald - 2018 - Journal of Evolutionary Biology - Wiley Online Library](https://onlinelibrary.wiley.com/doi/full/10.1111/jeb.13341) - Here, we use individual-based simulations to explore the effect of various types of environmental heterogeneity on the maintenance of genetic variation (VA) for a quantitative trait under stabilizing selection. We find that VA is maximized at intermediate migration rates in spatially heterogeneous environments and that the observed patterns are robust to changes in population size… Our results show that some combinations of spatial heterogeneity and migration can maintain considerably more variation than mutation–selection balance, potentially reconciling the discrepancy between theoretical predictions and empirical observations. However, given the narrow regions of parameter space required for this effect, this is unlikely to provide a general explanation for the maintenance of variation.

[Habitat corridors facilitate genetic resilience irrespective of species dispersal abilities or population sizes - Christie - 2015 - Evolutionary Applications - Wiley Online Library](https://onlinelibrary.wiley.com/doi/full/10.1111/eva.12255) – looked at corridor design and how it impacted genetic diversity, Ne, and differentiation of patches

[Social Sciences | Free Full-Text | A Literature Review on the Usage of Agent-Based Modelling to Study Policies for Managing International Migration (mdpi.com)](https://www.mdpi.com/2076-0760/11/8/356) – lit review on using ABMs to study international migration in humans

[Unpacking the Allee effect: determining individual-level mechanisms that drive global population dynamics (royalsocietypublishing.org)](https://royalsocietypublishing.org/doi/pdf/10.1098/rspa.2020.0350) – looked at global allee effects and how they can be translated to individual based mechanisms.

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Figure 2. Change in population demography measures with one migrant entering the population per generation in populations of various conservation rankings over time. (A) Proportion of alleles with migrant ancestry. (B) Observed heterozygosity of putatively neutral SNPs. (C) Fst as compared to the initialized focal population. (D) Fst as compared to the initialized source population.

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Figure 3. Change in population demography measures in the absence of population connectivity with populations of various conservation rankings over time. (A) Population size. (B) Observed heterozygosity of putatively neutral SNPs. (C) Fst as compared to the initialized focal population. (D) Fst as compared to the initialized source population.

*EXPECTED RESULTS*

*We expect that the results of migration on the population – fitness, inbreeding, lifetime reproductive success, heterozygosity and FST – will not necessarily change independently, but in tandem. For example, an increased frequency and intensity of migration will have a longer sustained benefit in population wide diversity as compared to little, irregular, or no migration events. We estimate that the average loss of genetic diversity occurs at a rate of 1/2N, in which N is the size of the diploid population, so that smaller populations have the greatest risk. In that same way, if one migrant is introduced into the population compared to five migrants in that same generation, the focal population with fewer migrants will have lower overall fitness benefits, higher inbreeding coefficients, and lower heterozygosity and allele frequencies.*

*We will also evaluate our model for insight into using migration as a predictive metric of population extirpation. We will specifically compare the predictive utility of migration of individuals with high and low fitness to examine population viability. We hope these analyses will add utility to on-going efforts to identify conservation need in wild populations and determining if translocation with selective migrants allows the population to maintain diversity for a longer duration.*

Chart

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Figure 1. Population size over time. Total number of individuals when a population goes through vulnerable (red), threatened (blue), and endangered (green) stochastic population declines.

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Figure 2. Best and worst case scenarios of genetic diversity during population subdivision. Heterozygosity over time when populations are connected via one migrant per generation (teal) and when populations are not connected (burnt red).

Graphical user interface, chart, line chart

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Figure 3. Increase in genetic diversity with assisted migration strategies. (A) Heterozygosity when adding 100 indv after habitat quality is restored (y = 151). (B) Heterozygosity when adding 25 indv four times after habitat quality is restored (y = 151, 165, 181, 195). (C) Heterozygosity when restoring the habitat via a corridor so that one migrant per generation can enter the population from year 151 on. (D) Averages of all 5 runs of the different migration rates depicted in panels A-C following habitat restoration.

Chart, line chart

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Figure 4. Average change in genetic diversity with varying migration rates and implementation times. Purple and pink lines depict the same migration rates (adding 100 indv once and 25 indv four times, respectively) during habitat restoration at the low population size (bright colors) and following restoration so that the population is permitted to grow (pastel colors).

Chart, line chart

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Figure 5. Change in population demographics over time with different staring allele frequencies (0.05 ≤ p ≤ 0.15 or 0.40 ≤ p ≤ 0.50) in both populations when there is one migrant per generation. (A) Heterozygosity over time with varying starting allele frequencies. (B) FST over time with varying starting allele frequencies. Black lines depict average change over time with no migrants.

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Figure 6. Average proportion of migrant introduced SNPs following assisted migration events.

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Figure 7. FST over time following assisted migration events. (A) Divergence of the focal population from the founding, initialized population over time. (B) Divergence of the focal and source populations following various translocation events.

Chart, histogram

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Figure 8. Average lifetime reproductive success over time.

Chart, radar chart

Description automatically generated Graphical user interface, chart, histogram

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SI Figure 1. The effect of having migrants preferentially chosen during sexual selection with zero migrants, one migrant per generation, and one migrant per generation following corridor construction. (A) Heterozygosity. (B) FST as compared to the initialized focal population. (C) FST as compared to the source population. (D) Proportion of migrant SNPs in the population. (E) Sex ratio. (F) FIS. (G) Average lifetime reproductive success. (H) points for LRS (to show that there is one indv that is skewing the RRS). (I) Relative lifetime reproductive success where the denominator is the individual with the greatest LRS in that run.