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RESEARCH ARTICLE

Demographic and genetic factors affect the use of translocation for evolutionary rescue: A case study of American chestnut using simulation

Sophia S. Stoltz | **Cortland K. Griswold** | **Brian C. Husband**

Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

Correspondence
Sophia S. Stoltz
Email: sstoltz@uoguelph.ca

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Abstract

1. For many plant species at risk, recovery depends on supplementing populations with adaptive genetic diversity through translocations but specific introduction strategies for maximizing success are rarely evaluated. American chestnut (*Castanea dentata*), a North American tree species whose populations have dramatically declined due to chestnut blight (caused by *Cryphonectria parasitica*), depends on evolutionary rescue to reverse its current trajectory. One approach to combating its decline is to supplement populations with more resilient genotypes (hereafter, resistant), derived from isolated individuals in natural populations or selectively bred individuals.
2. To identify the most effective restoration strategies, we evaluated the demographic and genetic conditions supporting population recovery using American chestnut as a case study. We examined two scenarios: natural recovery without translocation and the introduction of blight-resistant genotypes. Using existing data on chestnut demography and the genetic basis of resistance, we developed an individual-based simulation to model population dynamics over 500 years.
3. Our simulations indicate that evolutionary rescue is feasible but only under a restrictive set of conditions. Transplants with a high mean frequency of blight-resistance alleles, especially when spatially clustered, significantly reduced the probability of extinction over a 500-year period.
4. Achieving extinction probabilities below 10% was achieved through a combination of increased recruitment rates, the number of transplants and resistance, emphasizing the critical interplay between demographic and genetic parameters for recovery.
5. *Synthesis and applications*. These findings underscore the importance, complexity and flexibility of strategic translocations for ensuring the recovery of plant species limited by adaptive genetic diversity.

KEYWORDS
Castanea dentata, conservation, endangered species, evolutionary rescue, extinction risk, population modelling, translocation

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1 | INTRODUCTION

Ecological restoration aims to reverse the impacts of environmental degradation on populations and plays a central role in recovering species at risk (Holl & Aide, 2011). Restoration strategies range from passive regeneration to active interventions, designed to accelerate recovery, particularly when disturbances such as invasive species or low population sizes limit natural recovery (Chazdon et al., 2021; Holl & Aide, 2011; Prach et al., 2020). With approximately 26% of plant species in decline (IUCN, 2012), demand is growing for effective active management strategies, including habitat modification, population supplementation and restoring genetic diversity. An increasingly common restoration method is translocation—the intentional movement of individuals to establish or support populations and reduce extinction risk (Swan et al., 2018; Weeks et al., 2011). Such interventions are especially critical in systems facing persistent disturbances or slow recovery, including species with long generation times that cannot adapt quickly without assistance (Prach et al., 2020).

When active management of ecological or demographic processes is insufficient for recovery, evolutionary rescue may be required (Gomulkiewicz & Holt, 1995). Rescue refers to strategies that promote rapid adaptation to reverse population decline before extinction becomes likely, which depends on the presence of genetic variants with strong phenotypic effects that boost absolute fitness (Bell & Gonzalez, 2009; Gomulkiewicz & Holt, 1995). Migration or translocation of individuals with adaptive traits can increase the likelihood of rescue, especially for populations with limited standing genetic variation (Weeks et al., 2011). Selective breeding may be needed when suitable genotypes are absent in wild populations (Novak et al., 2021). Although theoretical and experimental studies highlight the roles of population size and genetic diversity in evolutionary rescue (Carlson et al., 2014; Gomulkiewicz & Holt, 1995), applying these concepts in real-world conservation efforts remains challenging (Klausmeier et al., 2020; Rodríguez-Trelles et al., 2013).

One species likely to require active restoration by evolutionary rescue is American chestnut (*Castanea dentata*). Once a dominant tree in eastern North American forests and an important economic source of nuts and lumber, chestnut populations suffered a catastrophic decline due to chestnut blight, caused by the fungal pathogen *Cryphonectria parasitica*. The fungus was introduced in ~1904 from east Asia and is now ubiquitous in deciduous forests, infecting chestnut trees as well as several secondary hosts (Rigling & Prospero, 2018). Chestnut blight has reduced American chestnut abundance by 90%–99%, and remnant survivors rarely reach reproductive age before succumbing to infection (Van Drunen et al., 2017). Most remnant trees persist only as stump sprouts, with little to no recruitment. Despite retaining high genetic diversity at neutral loci (Stoltz & Husband, 2023), genetically based blight resistance (to limit or prevent replication of the fungus) or tolerance (to maintain fitness in the presence of the fungus; Roy & Kirchner, 2000) appears limited in natural populations. Hence, the species remains functionally extinct throughout most of its former range and is listed as critically endangered by the IUCN and endangered in Canada.

Efforts to achieve recovery through creation of blight-resistant genotypes are well under way. The main approaches include backcrossing partially resistant Chinese chestnut (Burnham et al., 1986), applying hypovirulence to reduce pathogen virulence (Hebard, 1984) and developing transgenic lines with an oxalate oxidase wheat transgene that neutralizes the pathogen's oxalate toxin (McGuigan et al., 2020). Natural populations may also contain some relatively healthy appearing genotypes, but the heritability of these infrequent phenotypes has yet to be demonstrated. While the relative importance of tolerance versus resistance mechanisms in natural populations is not fully understood, chestnut breeding involving Asian germplasm typically uses resistance, and hence, we use the term here. While either strategy offers a mechanism for recovery (Sandercock et al., 2024), to date they have had limited success and use in restoration. Currently, no established guidelines exist for translocating American chestnut, or any other species at risk, for the purpose of achieving evolutionary rescue.

Simulation models offer a powerful tool for evaluating how demographic and genetic parameters affect translocation success, particularly when paired with empirical demographic information. The finite rate of population increase (λ), defined as the ratio of population size (N) at successive time points ($\lambda = N(t+1)/N(t)$), provides a concise measure of population trajectory. In Canada, demographic studies performed between 2001–2002 and 2014–2015 (a 13-year interval) revealed a declining population, with $\lambda = 0.817$, which corresponds to an approximate annualized λ of 0.985 in the presence of chestnut blight (Van Drunen et al., 2017). By contrast, a largely blight-free population in central Maine, USA, demonstrated growth, with $\lambda = 1.03$ calculated on an annual basis (Elwood, 2014). These matrices allow for simulations of translocation outcomes, grounded in species-specific life history traits and environmental context.

In this study, we use an individual-based model (IBM) to simulate the demographic and genetic dynamics of American chestnut in southern Canada. The model tracks individuals' genetic attributes and links them to vital rates (e.g. growth, reproduction, survival and dispersal), enabling the exploration of population trajectories under various translocation strategies (Huston et al., 1988). Using empirical demographic data from previous surveys, we address three key questions: (1) How do the number, degree of resistance, spatial arrangement and recruitment rates of introduced trees affect extinction risk? (2) What combinations of these parameters maintain extinction probabilities below 10%? (3) How many trees from the current breeding programme are needed to achieve evolutionary rescue?

2 | MATERIALS AND METHODS

Chestnut populations were simulated in two stages. First, a baseline population was simulated with the estimated vital rates of the current Canadian population, which allowed us to validate the simulated population dynamics against field estimates. Then the simulation was expanded to include translocations at various abundances,

spatial arrangements and levels of resistance to blight, to explore the effect of interactions between demographic and genetic characteristics on evolutionary rescue.

2.1 | Baseline model

We simulated the population dynamics of American chestnut using vital rates from a low-resistance population in Ontario, Canada (Van Drunen et al., 2017). Individuals were randomly assigned to a 100 km × 300 km grid, approximating the species' range in southern Canada. The baseline population size was set to 2200 individuals, randomly distributed among five life stages according to observed proportions. Stages (Stg) were defined by age and size (diameter at breast height (DBH) as: Stg0, <13 years; Stg1, ≥13 years, DBH ≤2 cm; Stg2, ≥13 years, DBH 2–10 cm; Stg3, ≥13 years, DBH 10–20 cm; Stg4, ≥13 years, DBH ≥20 cm). The 13-year criterion reflects the interval between the two field surveys (2001–2002 and 2014–2015) and distinguished saplings (stages 0 and 1) from other stages. Stage transitions (stasis, growth, regression, probability of survival and reproduction) were taken from the transition matrix based on the assessment of 650 trees (Van Drunen et al., 2017). Recruitment rates, representing the combined likelihood of flowering, producing a seed and seedling establishment, were also taken from Van Drunen et al. (2017). These demographic transitions and rates, originally based on a 13-year survey interval, were converted to a yearly timestep (Appendix 1). Reproductive output was modelled as a Poisson-distributed number of offspring, with means equal to the annual recruitment rate. Although recruitment was reported for trees in stage 2, it was set to zero in the baseline model due to its low probability.

Each individual was assigned a blight-resistance genotype under a biallelic, three-locus model (Kubisiak et al., 1997, 2013). Genotypes consisted of pairs of alleles at each locus (e.g. genotype = [[0,0], [0,0], [0,0]]), where '0' indicated a wildtype (non-resistant) allele and '1' indicated a blight-resistant allele. Resistance ranged from 0 to 6, with additive allele effects such that resistance increased proportionally with the number of resistance ('1') alleles across the three loci. All baseline individuals carried only wildtype alleles, representing low or no resistance observed in current natural populations. We also conducted a supplementary simulation to evaluate the robustness of our results to assumptions about genetic architecture (30 vs. three-locus model) and trait heritability ($h^2 = 1.0$, 0.7 and 0.4), motivated by studies suggesting that blight resistance is likely polygenic (Fan et al., 2024; Westbrook et al., 2020). Details of these simulations are described in Appendix 5.

New recruits were assigned both a genotype and a spatial position in the simulation landscape. The genotype of each recruit was generated by randomly choosing a pollen donor from among all reproductive trees within 100 m of a given maternal parent (Russell, 1987), with probability weighted by distance according to a negative exponential dispersal kernel. Offspring genotypes were formed by randomly selecting one allele per locus from each parent. Seed dispersal distances from the mother tree were drawn from a negative exponential distribution with a maximum limit of 300 m, consistent with evidence of limited dispersal in chestnuts (Heinrich, 2014). Dispersal direction was randomly assigned. To account for low establishment success near the maternal parent due to competition, a minimum dispersal distance of 6.096 m (20 feet) from all existing individuals was enforced. If a recruit's location fell within this exclusion zone, new spatial coordinates were generated.

2.2 | Validation of the baseline model

To validate the baseline model, we calculated the population growth rate (λ) and predicted stable stage distribution ($\overline{w}$) using the leading eigenvalue and corresponding eigenvector of the annual transition matrix. Initial adjustments were made to better reflect annual demographic processes, including revised recruitment rates and transition probabilities (Appendix 2). The final matrix closely matched the original λ and $\overline{w}$ reported by Van Drunen et al. (2017) (Appendix 3; Figure 1), and the predicted stable stage distribution aligned with outcomes from simulations of a 650-individual population across 1000 replicates and 500 years (Appendix 3; Table 1).

2.3 | Addition of transplants with baseline and resistant genotypes

To explore the potential for evolutionary rescue, we introduced translocated individuals (transplants) with different levels of blight resistance into the baseline population. Transplants were introduced at the start of the simulation (stage 0) and spatially placed to avoid overlap with baseline individuals.

Genotype effects were modelled by adjusting the baseline transition matrix according to each individual's genotype. Demographic characteristics for partially resistant trees were derived from a 'blight-free' population in Maine, USA (Elwood, 2014), which reported a nine-stage transition matrix with annual transition and fecundity rates. To align with the five-stage structure used by Van Drunen et al. (2017), Elwood's stages were collapsed by averaging their transition probabilities across corresponding classes. Because some stages in Elwood (2014) reported zero mortality despite an overall survival of 99.9%, we reassigned a small proportion (0.001) of the probability to stasis, the highest within-stage transition probability, as a death rate for those stages to ensure consistency in the matrix. Recruitment rates tested in our simulations were gradually increased from Van Drunen et al. (2017) to reflect enhanced fecundity with increasing resistance. The resulting matrix emphasized stasis and reduced mortality, representing a demographic endpoint for fully resistant individuals (Appendix 4).

To assign demographic properties to individuals with full or partial blight resistance (ranging from 1 to 6 resistance alleles), each of the three loci were evaluated independently based on homozygosity. For loci homozygous for the wildtype allele ([0,0]), the individual's

TABLE 1 List of parameters and their possible values included in the simulation of American chestnut populations.

Parameter type	Parameter name	Values
Spatial	Spatial distribution of baseline American chestnuts	• Random • Clustered
	Spatial distribution of transplants	• Random • Clustered
	Number of clusters (only applicable when spatial distribution is 'Clustered')	• 1 • 4 • 8
Demographic	Number of transplants at year 0	• 0 • 200 • 300 • 400 • 500
	Paired recruitment rates for stages 3 and 4, respectively	• Stg3: 0.002882; Stg4: 0.008837 • Stg3: 0.005764; Stg4: 0.017674 • Stg3: 0.01; Stg4: 0.03 • Stg3: 0.015; Stg4: 0.035 • Stg3: 0.02; Stg4: 0.04 • Stg3: 0.025; Stg4: 0.045 • Stg3: 0.03; Stg4: 0.05
Genetic	Mean resistance allele frequency in the translocation	• 0 • 0.2 • 0.3 • 0.4 • 0.5 • 0.6 • 0.7 • 0.8

transition probabilities followed the baseline matrix, adjusted to a single locus ($\frac{P_{i,j}}{3}$). For loci homozygous for the resistance allele ([1,1]), transition probabilities were calculated as the sum of the baseline probabilities adjusted to a single locus and the difference between the Elwood matrix and the Van Drunen matrix, further adjusted to a single locus ($\frac{P_{i,j}}{3} + \frac{(\mathrm{EW}_{\mathrm{matrix}} - \mathrm{VD}_{\mathrm{matrix}})}{3}$). Heterozygous loci ([0,1] or [1,0]) were treated as co-dominant, contributing half the adjustment of a homozygous resistance locus added to the probabilities of the baseline, adjusted to a single locus ($\frac{P_{i,j}}{3} + \left(0.5 * \frac{(\mathrm{EW}_{\mathrm{matrix}} - \mathrm{VD}_{\mathrm{matrix}})}{3}\right)$). The final genotype-specific transition matrix was obtained by summing the contributions of all three loci.

2.4 | Parameter combinations

Simulations tested the effect of six parameters (or conditions) on population dynamics: three spatial, two demographic and one genetic (Table 1). The spatial parameters included (1) the distribution of baseline individuals, (2) the distribution of transplants and (3) the number of spatial clusters, which applied to both baseline and translocated trees in clustered scenarios. In clustered arrangements, baseline trees were evenly divided among clusters, each located within a 17.5 km radius of a randomly generated focal point, reflecting localized patterns in Van Drunen et al. (2017). A random distribution introduced individuals uniformly across the landscape, while clustered transplants were introduced within 30 m (mean pollen dispersal distance) of baseline trees. All spatial combinations were tested, except that clustered transplants were only paired with clustered baseline arrangements. Demographic parameters included the number of transplants and paired recruitment rates per tree for stages 3 and 4. The genetic parameter was the mean frequency of the resistance allele in translocated trees. All demographic and genetic combinations were fully crossed.

2.5 | Running the model and response variables

Each parameter combination was simulated for 500 years or until the population reached 10,000 individuals, across 1000 replicates. We recorded annual values for population size, genotypes, spatial coordinates and life stage. All models were developed using custom scripts in Python v3.10 and computation was performed on Digital Research Alliance of Canada's Graham and Fir high-performance computing clusters.

We calculated mean annual population size and mean resistance allele frequency across all replicates for each parameter set. Extinction risk at time t ($G(t)$) was evaluated using Lande's diffusion approximation formula (Lande, 1993) as applied by Morris and Doak (2002): $G(t) = \Phi\left(\frac{-d-\mu t}{\sqrt{\sigma^2 t}}\right) + \exp\left(\frac{-2\mu d}{\sigma^2}\right)\Phi\left(\frac{-d+\mu t}{\sqrt{\sigma^2 t}}\right)$, where $d = \log_e(N_c) - \log_e(N_x)$, with $N_x = 50$ (quasi-extinction threshold), N_C as mean population size, μ as the mean log population growth rate, and σ^2 as its variance.

To identify parameter combinations most conducive to evolutionary rescue, we applied a 10% extinction probability threshold, consistent with the IUCN Red List criteria for threatened species (IUCN, 2012). Unlike the standard 100-year assessment period, we applied this threshold over a 500-year timespan for a more conservative evaluation.

2.6 | Individual effect of each parameter

To illustrate the impact of each parameter on extinction probability, we plotted 500-year timeseries while varying one parameter at a time, holding others constant. We assessed the effects of transplant number, mean resistance allele frequency in the translocation, recruitment rate and transplant spatial distribution. Default settings across analyses were recruitment rates of 0.015 (stage 3, reflecting a 1.5% chance an individual contributes at least one recruited offspring within a given year) and 0.035 (stage 4), a resistance allele frequency of 0.5, and 400 transplants. For all but the analysis of spatial distribution, both baseline and transplant individuals were randomly distributed; in that analysis, baseline individuals were clustered into 4 groups.

2.7 | Combined effect across parameters

We assessed the combined effects of the manipulated parameters on 500-year extinction probability using several visualizations. The influence of transplant number and mean resistance allele frequency of the translocated trees on extinction under each spatial treatment (random vs. clustered) was illustrated using a boxplot. A bar plot was used to demonstrate the parameter combinations (transplant number, resistance allele frequency in the translocation and recruitment rate) resulting in <10% extinction probability at 500 years. To evaluate whether these combinations showed diagnostic features of evolutionary rescue, we plotted a timeseries of mean population size by stage and resistance allele frequency for one specific parameter set: recruitment rates of 0.03 (stage 3) and 0.05 (stage 4), mean resistance allele frequency in the translocation of 0.6, and 500 clustered transplants, with baseline and translocated individuals in one cluster.

We assessed how spatial, demographic and genetic parameters influenced 500-year extinction probability using a logistic regression. Extinction probability (treated as a proportion) was modelled as the response variable using a logit link and a binomial family. Predictor variables included the following: spatial distribution of baseline trees; spatial distribution of transplants; number of clusters; paired recruitment rates for stages 3 and 4, number of transplants; mean resistance allele frequency in transplants; and an interaction term between the latter two. All predictors were numeric except for the two spatial terms which were coded as categorical variables. Numeric variables were centred and scaled for effect size comparison. Model diagnostics were conducted using the R package DHARMa v.0.2.4 (Hartig, 2019), and multicollinearity was evaluated via variance inflation factors (VIF) using car v.3.1–0 (Fox & Weisberg, 2019), with no modifications needed. Predictor significance was assessed using standardized β coefficients, standard errors, z-values and p-values.

2.8 | Translocation size for recovery

Resistance attained in current backcross breeding programmes, indicated by canker severity closer to wildtype American chestnut and lower than the ~50% resistance of F_1 hybrids (*C. dentata*×*C. mollissima*), falls below the ≥0.5 threshold required for extinction probabilities <10% in our simulations (Steiner et al., 2017). To evaluate recovery potential at this resistance level, we conducted additional simulations introducing up to 4000 transplants into a 2200-tree baseline population (with the same stage structure and four spatial clusters), under a subset of recruitment rates for stages 3 and 4 (0.002882–0.025 and 0.008837–0.045, respectively), and mean resistance allele frequencies of 0.3–0.45. Each parameter set was simulated for 500 years or until the population reached 10,000 individuals and replicated 1000 times.

3 | RESULTS

3.1 | Impact of population parameters on extinction probability

Varying each parameter independently while holding others constant revealed that the four focal variables had distinct and unequal effects on the timing and likelihood of population extinction (Figure 1). Increasing the number of transplants and mean resistance allele frequency in the translocations, and clustering transplants near baseline individuals delayed the onset of extinction (Figure 1a,b,d). In contrast, when recruitment rate was varied alone within the range of parameter combinations presented in this figure, population trajectories were indistinguishable across recruitment values (Figure 1c).

Logistic regression of all simulation runs combined revealed that spatial, genetic and demographic parameters significantly influence extinction probability at year 500, collectively explaining 99.4% of the variance (Table 2). Lower extinction probabilities were associated with clustered transplants ($\beta=-13.790$, $z=-3.751$, $p=1.76\times10^{-4}$), higher mean resistance allele frequency ($\beta=-5.497$, $z=-6.634$, $p=3.26\times10^{-11}$), increased recruitment rate ($\beta=-4.985$, $z=-7.614$, $p=2.66\times10^{-14}$) and greater number of transplants ($\beta=-2.027$, $z=-2.842$, $p=4.48\times10^{-3}$). However, the spatial treatment of baseline individuals ($\beta=-0.041$, $z=-0.006$, $p=0.995$), the number of spatial clusters ($\beta=0.171$, $z=0.712$, $p=0.477$) and the interaction between the number of transplants and the mean resistance allele frequency ($\beta=-0.670$, $z=-0.990$, $p=0.322$) were not significant predictors of extinction probability at year 500.

While no statistical interaction effects were detected, the independent variables differed in their relative effect sizes on extinction probability. Among them, resistance allele frequency and spatial arrangement of transplants had the strongest individual impacts

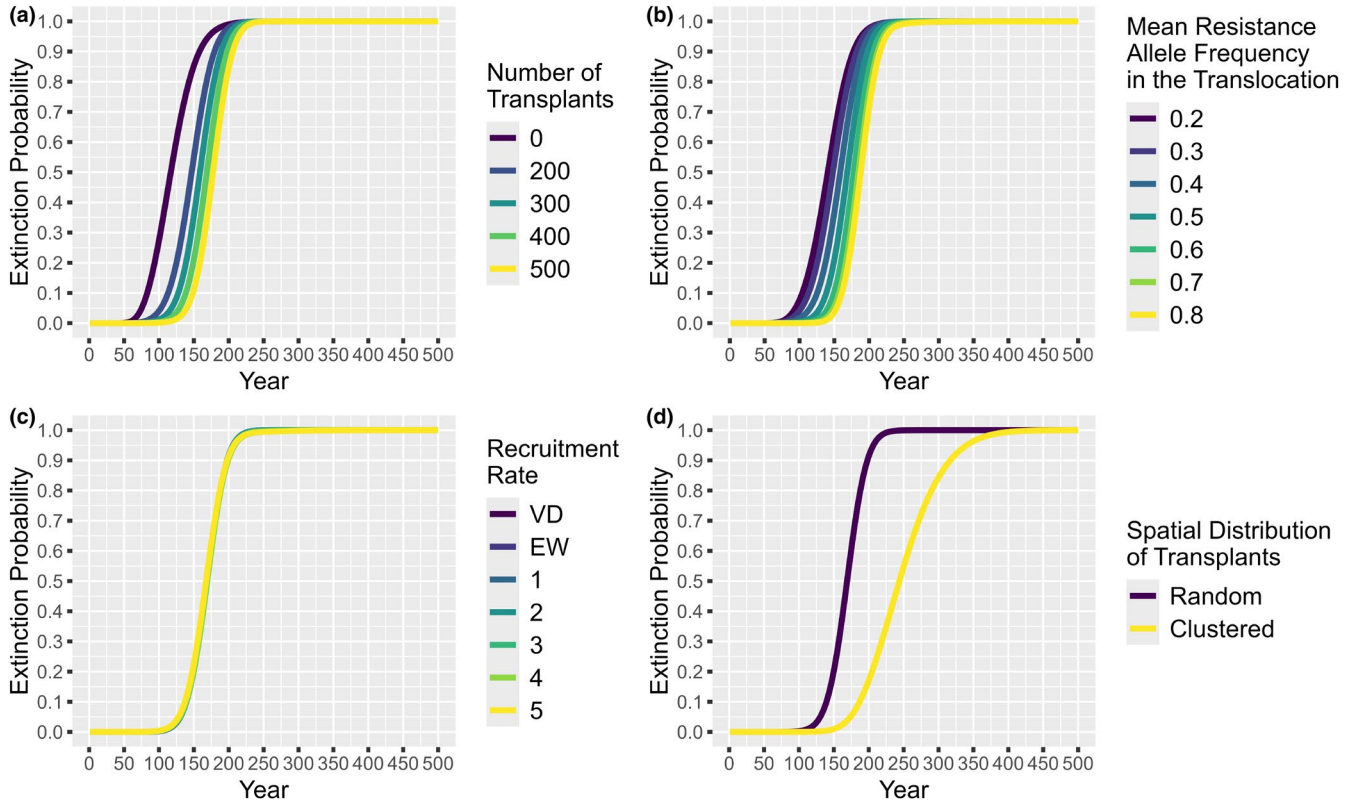


FIGURE 1 Individual effect of four parameters on the 500-year extinction probability. (a) Number of transplants, (b) mean blight-resistance allele frequency in the translocation, (c) recruitment rate, (d) spatial distribution of transplants.

TABLE 2 Logistic regression analysis of the probability of extinction at year 500 in relation to all population parameters.

Parameter type	Parameter name	Standardized coefficients (β)	Standard error	*z*-value	*p*-value
Demographic	Number of transplants	−2.027	0.713	−2.842	4.48×10^{-3}
	Recruitment rate	−4.985	0.655	−7.614	2.66×10^{-14}
Spatial	Spatial distribution of transplants	−13.791	3.677	−3.751	1.76×10^{-4}
	Spatial distribution of baseline individuals	−0.041	6.460	−0.006	0.995
	Number of spatial clusters	0.171	0.240	0.712	0.477
Genetic	Mean resistance allele frequency in the translocation	−5.497	0.827	−6.634	3.26×10^{-11}
Demographic × Genetic Interaction	Number of transplants × Mean resistance allele frequency in the translocation	−0.670	0.706	−0.990	0.322

Note: Standardized β coefficients, standard errors, *z*-values and *p*-values quantify the effect size and precision of the associations.

(Table 2). When resistance allele frequencies were ≥0.5 and transplants were spatially clustered, extinction probabilities approached zero by year 500 (Figure 2). This pattern highlights the additive effects of spatial and genetic parameters in promoting persistence. We note that supplementary simulations with a 30-locus architecture and varying heritability showed the same directional effects, though mean extinction probabilities were modestly higher: ~3.7% greater under the 30-locus model (95% CI: 1.0%–7.0%), and elevated further at lower heritability ($h^2=0.4$) relative to moderate or complete heritability ($h^2=0.7$–1.0); see Appendix 5 and Figure S2. These results indicate that the main conclusions are robust, but that greater genetic complexity and reduced heritability raise baseline extinction risk, particularly under scenarios with fewer transplants or lower recruitment rates (Appendix 5; Figure S3).

3.2 | Parameter combinations maintaining extinction risk below 10%

Extinction probabilities fell below the IUCN threshold of 10% under a restricted set of parameter combinations. Specifically, it occurred when transplants were spatially clustered, had a mean resistance

allele frequency ≥0.5, and recruitment rates of ≥0.02 and ≥0.04 for life stages 3 and 4, respectively (Figure 3). As the resistance allele frequency in transplants increased, lower recruitment rates and fewer transplants were required to remain below the extinction threshold.

To illustrate the trajectory of populations with extinction probabilities below 10%, we arbitrarily selected one parameter set, with 500 clustered transplants, a mean resistance allele frequency of 0.6, baseline population of 2200 trees, and recruitment rates of 0.03 (stage 3) and 0.05 (stage 4), we tracked population dynamics over 500 years (Figure 4). The population declined sharply over the first 200 years, stabilized around 375–400 individuals for ~125 years, then increased steadily after year 325 (Figure 4a). A shift in stage distribution occurred at year 13, as individuals aged into later stages, eventually resulting in a population structure with a larger proportion of individuals in stages 0 and 4 over time (Figure 4b). Concurrently, the mean resistance allele frequency rose to 0.79 before the end of the simulation (Figure 4a).

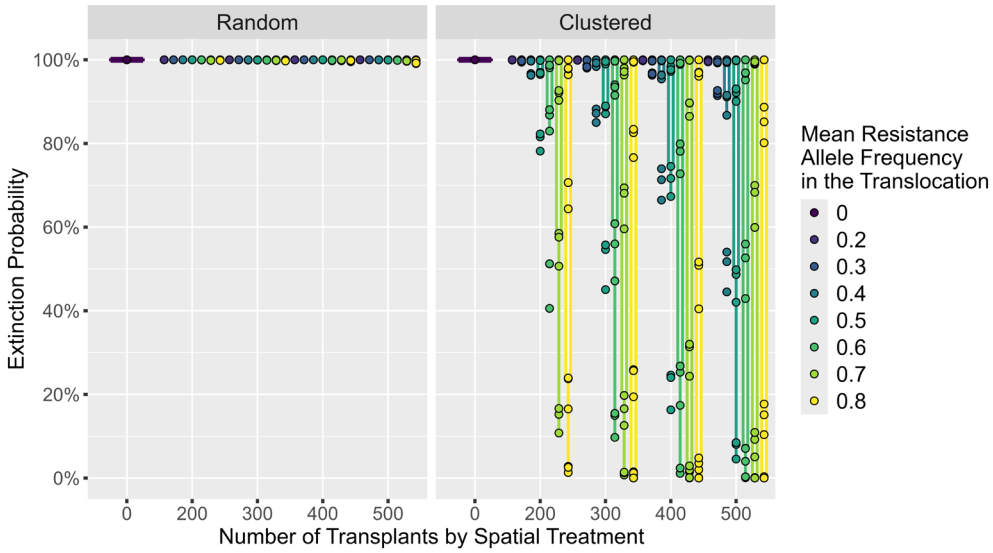


FIGURE 2 Cumulative effect of number of transplants and mean blight-resistance allele frequency in the translocated trees on the 500-year extinction probability of simulated American chestnut. Results are presented for transplants in random and clustered spatial treatments. Points represent mean extinction probability across 1000 simulation replicates.

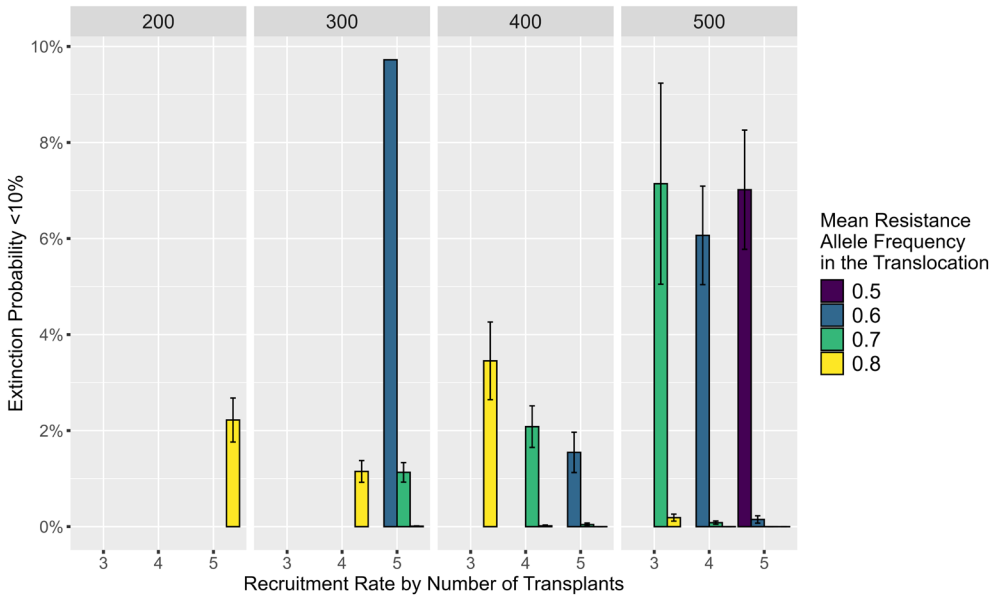


FIGURE 3 Probability of extinction at 500 years (*y*-axis; <10%) as a function of recruitment rate and mean blight-resistance allele frequency in the translocation (*x*-axis). Results are presented by number of transplants (200, 300, 400 and 500) and illustrate extinction probabilities below 10%, with standard error bars. Recruitment rates on the *x*-axis are defined categorically as: 3 = 0.02 (stage 3) and 0.04 (stage 4); 4 = 0.025 (stage 3) and 0.045 (stage 4); 5 = 0.03 (stage 3) and 0.05 (stage 4).

3.3 | Number of transplants needed for recovery at breeding programme levels of resistance

Because the reported blight-resistance levels in breeding programmes are below 0.5 (Steiner et al., 2017), our simulations tested translocations with resistance values within the range of 0.3–0.45. At these levels, the number of transplants necessary for evolutionary rescue is much higher than the 500 used in our simulations (Figure 5). At the upper resistance level (0.45), at least 1000 transplants are needed, assuming recruitment rates ≥0.025 (stage 3) and

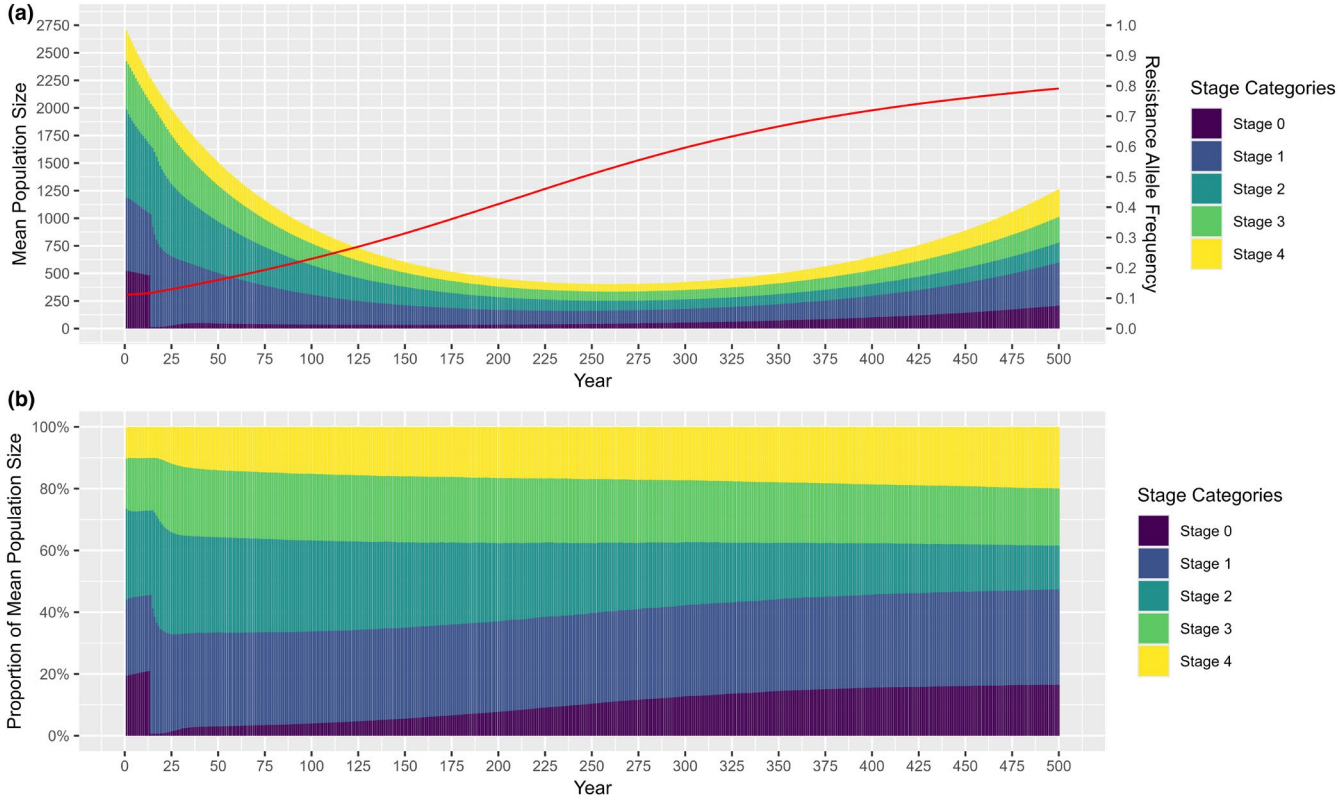


FIGURE 4 (a) Mean population size by stage and (b) proportion of mean population size by stage over 500-years across 1000 replicates from a simulation with recruitment rates of 0.03 (stage 3) and 0.05 (stage 4), a mean blight-resistance allele frequency of 0.6 in the translocation, and 500 transplants arranged in a single clustered spatial distribution for both baseline and transplanted trees. The red line in (a) represents the population mean frequency of the blight-resistance allele.



FIGURE 5 Cumulative effects of recruitment rate, number of transplants, and mean blight-resistance allele frequency in the translocation on the 500-year extinction probability (<10%). Results are presented by number of transplants (1000, 1500, 2000, 3000 and 4000). Recruitment rates are defined as their values in the simulation: 2=0.015 (stage 3) and 0.035 (stage 4), and 4=0.025 (stage 3) and 0.045 (stage 4).

≥0.045 (stage 4). With the same recruitment rates, increasing the number of transplants to 4000 allows for a lower resistance allele frequency (0.3) to still achieve persistence.

4 | DISCUSSION

Population simulations reveal that extinction probabilities below 10% are achievable in American chestnut using translocations, but only under restrictive combinations of spatial, demographic and genetic conditions. Without translocations, extinction always occurred. Translocations without elevated blight resistance also never achieved extinction probabilities <10%. Introducing partially resistant transplants can elevate overall population blight resistance, improve recruitment and survival and enable adaptive genotypes to spread before the population declines irreversibly, offering key insights for conservation management.

4.1 | Evidence of evolutionary rescue

Simulated populations followed a range of trajectories, with those showing extinction probabilities below 10% displaying patterns consistent with evolutionary rescue (Figures 4 and 5). As defined by Vander Wal et al. (2013), evolutionary rescue involves four phases: (1) initial population decline following environmental stress, (2) adaptation via phenotypic change and (3) subsequent recovery. These phases were observed when translocated individuals with partial resistance were introduced (Figure 4). The initial phase is depicted by a sharp population decline as susceptible wildtype individuals succumb to blight. Around year 13, transplants approach reproductive maturity, which results in some recruitment, increasing blight-resistance allele frequencies and stabilizing population size. This marks the adaptation phase, driven by selection for resistant genotypes. By year 325, the frequency of resistance alleles surpasses 0.65, and the population size begins to rebound, reaching its original size at some point beyond year 500. All simulated populations that met the <10% extinction threshold demonstrated this characteristic trajectory. These demographic shifts and the rise of the adaptive allele frequency are consistent with evolutionary rescue (Bell & Gonzalez, 2009) achieved through multigenerational increases in blight resistance in American chestnut (Carlson et al., 2014; Gustafson et al., 2017).

The timing of recovery aligns with previous studies of evolutionary rescue. Theoretical and experimental evidence suggests evolutionary rescue can occur within 25 generations in large populations with limited stochasticity (Bell & Gonzalez, 2009). For American chestnut, with an estimated 20-year generation time (Paillet & Rutter, 1989), this corresponds to ~500 years. By introducing pre-adapted transplants at the simulation's onset, the need for mutation-driven adaptation is effectively bypassed, thereby accelerating evolutionary rescue timelines (Vander Wal et al., 2013).

The genetic architecture of blight resistance likely influences the dynamics of evolutionary rescue. Our model assumes resistance is encoded by three unlinked loci, which accounts for roughly 40% of observed variation in *C. parasitica* canker severity (Kubisiak et al., 1997, 2013). However, an increasing body of work suggests that blight resistance is likely polygenic. Observations of the third backcross generation (BC_3F_2) in the American Chestnut Foundation's breeding programme support this, revealing a trade-off between blight resistance and the proportion of the *C. dentata* genome (Westbrook et al., 2020). More recently, this pattern has been attributed to a moderately complex genetic architecture underlying blight resistance, with 31 resistance QTLs identified across 12 chromosomes (Fan et al., 2024). If resistance is controlled by a few loci of large effect, evolutionary rescue may occur more rapidly but at higher risk of allele loss due to drift (Kardos & Luikart, 2021; Yamamichi, 2022). In contrast, if resistance is highly polygenic, with many loci each of small effect, the trait may provide greater evolutionary potential and resilience, but adaptation proceeds more slowly and favourable allele combinations are more easily broken apart by recombination (Uecker & Hermisson, 2016). Consistent with these expectations, supplementary simulations incorporating a more polygenic (30-locus) architecture and reduced heritability produced consistently higher extinction probabilities than the three-locus model (Appendix 5), indicating that more diffuse genetic control and weaker genotype–phenotype mapping both diminish the likelihood of evolutionary rescue. While these analyses did not alter the qualitative conclusions of the main model or the relative importance of the demographic, genetic and spatial parameters, they indicate that our three-locus model likely underestimates genetic complexity and therefore may underestimate the true risk of extinction. Improving our understanding of the genetic basis of blight resistance remains crucial for setting realistic expectations around the timeline and feasibility of evolutionary rescue.

4.2 | Effectiveness of translocations for enhancing population persistence

In our simulations, several demographic, spatial and genetic parameters significantly influenced long-term American chestnut recovery. Among them, the spatial arrangement of transplants had the strongest effect on extinction probability (Table 2). Clustering transplants with baseline populations consistently reduced extinction risk and slowed decline though never achieved evolutionary rescue (≤10% extinction) on its own. Higher extinction risk under the random spatial treatment likely reflects the sparse tree distribution and greater isolation, which slows the spread of resistance alleles and the impacts of demographic stochasticity and Allee effects which can drive rapid extinction before transplants establish (Deredec & Courchamp, 2007). Clustering increases local density, reproduction and gene flow, helping overcome mate limitation. Elevated frequencies of blight-resistance alleles in transplants also reduce extinction risk by increasing the spread of adaptive alleles and improving population mean fitness. While our model excluded environmental heterogeneity, combining broad genetic backgrounds with blight resistance remains a robust strategy for long-term adaptation.

Recruitment rate also strongly influenced extinction probability (Table 2). Despite higher numbers of reproductive trees in Canadian populations than in the United States, low recruitment continues to limit recovery (Van Drunen et al., 2017). In small, endangered populations, poor recruitment restricts growth, dispersal and the infusion of new genetic diversity required for adaptation and evolutionary rescue (Volis, 2019). Chestnut blight has historically prevented most trees from reaching reproductive maturity, restricting recruitment and mate availability. Even with increased transplant numbers and resistance, recovery is unlikely without improved recruitment (Figures 3 and 5). Larger transplant numbers consistently lowered extinction risk and delayed extinction, aligning with previous findings that higher introduction numbers improve establishment and buffer against stochasticity (Griffith et al., 1989; Lande, 1988; Whitehead et al., 2023).

No single spatial, demographic or genetic parameter alone was sufficient to achieve evolutionary rescue (defined as <10% extinction probability). Instead, rescue was only observed when multiple parameters were adjusted in combination and acted additively. For instance, combining high blight-resistance allele frequencies with elevated recruitment rates and spatially clustered transplants consistently enhanced survival, reproduction and establishment, increasing adaptive allele frequency and facilitating recovery.

Certain parameter combinations were particularly effective at lowering extinction probabilities (Table 2). For example, spatially clustered transplants with a mean resistance allele frequency ≥0.5 enabled recovery with up to 500 translocated individuals (Figure 3). In contrast, a resistance level of 0.4 required larger numbers of transplants to achieve similar outcomes (Figure 5). These results indicate that while blight resistance is critical, constraints on resistance levels achievable can, to some extent, be offset by increasing transplant numbers or improving recruitment. However, if resistance is too low to allow survival to reproductive maturity, even high numbers of transplants or favourable spatial arrangements cannot ensure persistence. Our simulations identified the minimum viable combination for rescue as 500 clustered transplants with a blight-resistance allele frequency of 0.5, and recruitment rates of 0.03 and 0.05 in stages 3 and 4, respectively. When transplant numbers are constrained, higher blight resistance can compensate. For example, introducing 200 individuals with a mean frequency of the blight-resistance allele of 0.8 in a clustered spatial arrangement was sufficient to maintain extinction probabilities below 10% and achieve full recovery (Figure 3). Supplementary simulations incorporating more polygenic resistance and reduced heritability showed the same general trends but required even higher resistance levels or greater transplant numbers to achieve comparable outcomes (Appendix 5). Ultimately, while adjustments in transplant number and recruitment can buffer limitations to blight resistance to some extent, a minimum threshold of adaptive allele frequency above wildtype is essential for rescue.

4.3 | Management implications

For many species at risk, translocations offer a viable strategy to counter declines caused by persistent threats by increasing population size and introducing resilient phenotypes. However, success likely depends on not only the quantity and spatial configuration of transplants but also their genetic composition. In our study, translocations without elevated relative fitness are insufficient to alter population trajectories, a scenario likely to occur in any species for which the causes of endangerment are severe as well as ubiquitous. These circumstances underscore the need to balance demographic, spatial and genetic aspects of translocations to meet the desired extinction thresholds.

For chestnut specifically, our simulations show that evolutionary rescue is most feasible when phenotypic resistance exceeds 0.5 (relative to Chinese chestnut). However, current breeding programmes report phenotypic resistance below 0.5 (Steiner et al., 2017; Westbrook et al., 2020). Evolutionary recovery at these levels is still possible but requires a compensatory increase in transplant numbers, recruitment and spatial clustering. For example, achieving <10% extinction probability over 500 years requires 1000 transplants at a resistance of 0.45, and 2000 transplants at a frequency of 0.3 (Figure 5). As breeding programmes advance, via phenotypic selection, genomic selection or transgenic approaches, and levels of resistance attained increase, the number of transplants necessary for recovery is expected to decline (Clark et al., 2023; Steiner et al., 2017; Westbrook et al., 2020). Achieving recovery also requires a 5- to 8-fold increase in recruitment but this is likely to be correlated with population-wide resistance, which will increase the frequency of reproductive individuals and their fecundity. Management actions such as canopy thinning or vegetation control could be used to further enhance recruitment, though the impact of such strategies, in combination with translocations, remains to be quantified.

Understanding the evolutionary dynamics of populations with the addition of translocations is relevant to many species whose recovery depends on the introduction of adaptive genetic variation. Whether facing invasive pathogens, emerging infectious diseases or rapidly shifting environments, restoration programmes must often balance translocation size, genetic composition and spatial placement to achieve population persistence. The strong interactions we observe among propagule pressure, spatial structure, genetic architecture and heritability likely echo factors affecting a wide range of species, from butternut threatened by butternut canker (Pike et al., 2021) to beeches with beech bark disease (Stephanson & Coe, 2017), amphibians facing chytrid fungi (Scheele et al., 2021) and corals requiring thermal tolerance (Roper et al., 2025). As such, the framework presented here may help guide translocation planning and genetic-management strategies across a range of conservation contexts.

Beyond the biological attributes of the translocations, other factors, not included in our simulations, may influence recovery feasibility. First, our simulations assume a spatially and temporally uniform environment, yet environmental variation can influence the impact of threats such as pathogen virulence and host response (Clark et al., 2019; Lione et al., 2022). While the degree and mechanisms by which environmental conditions influence organismal health remain poorly understood in many systems, correlative evidence from chestnut suggests that health outcomes and the incidence of recovery or

healing are influenced by local conditions (Van Drunen et al., 2018). Incorporating environmental effects will improve the accuracy of predictive models and will likely increase variation in the success of translocations. In the meantime, such information may be used to inform decisions about which locations will maximize translocation success.

Finally, there are an array of socioeconomic factors to consider when implementing a translocation programme. Large scale translocations require substantial human and financial resources, a source and steady supply of suitably adaptive planting stock, access to suitable habitat (Environment and Climate Change Canada, 2019; Tindall et al., 2004; Van Drunen et al., 2018) and an evaluation process to monitor and maintain plantings. Also, ethical considerations must not be underestimated, especially given the relatively rare use of translocations by plant conservationists (McCune et al., 2024). Introducing human-manipulated genotypes on a large scale must be weighed against the risks of disrupting existing population structure, altering native ecosystems, displacing existing species or creating conditions that benefit invasive species (Hoffmann et al., 2021; Laikre et al., 2010). These concerns require engagement with all stakeholders/rightsholders to ensure restoration efforts are socially and ecologically responsible. Provided these challenges are carefully addressed and recovery efforts are supported by sufficient resources and community involvement, our findings suggest that long-term recovery via evolutionary rescue is attainable under the right circumstances.

AUTHOR CONTRIBUTIONS

Sophia S. Stoltz led the conceptualization, methodology, data collection, analysis and visualization, and wrote the original draft. Cortland K. Griswold assisted with methodological design and provided computational resources and supervision. Brian C. Husband contributed to conceptualization and supervision, and secured funding. All authors contributed critically to reviewing and editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All simulation data supporting this study and the complete model source code required to reproduce the results are archived in the Zenodo Digital Repository at https://doi.org/10.5281/zenodo.18614582 (Stoltz et al., 2026b) and https://doi.org/10.5281/zenodo.18614113 (Stoltz et al., 2026a), respectively.

ORCID

Sophia S. Stoltz https://orcid.org/0000-0002-5487-8463

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix 1. Transition matrix conversion from Van Drunen et al. (2017).

Appendix 2. Technical adjustments for baseline transition matrix validation.

Appendix 3. Validation of the baseline transition matrix and simulation model.

Appendix 4. Difference between the Elwood matrix (EW) and the Van Drunen matrix (VD).

Appendix 5. Test of additional loci at varying trait heritability values in the simulation model.

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