
Modeling Evolutionary Rescue Under Gradual Environmental Change and Invasive Species Dynamics

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Abstract

Gomulkiewicz and Holt [10] introduce three models (two-step, quantitative genetic, and diploid locus) to analyze situations in which evolution by natural selection can rescue a threatened population from extinction. However, their models do not capture well-known extinction risk factors, including climate change, invasive species, and loss in genetic diversity. We build off of these models to account for these factors, finding that the gradual threat of climate change can increase the possible scenarios for rescue, while invasive species decrease the possible scenarios. Furthermore, we find that population recovery comes at the loss of tremendous genetic diversity, placing it at greater disease risk. Our models numerically validate extinction risk factors and can inform conservation biologists on good practices for rescuing threatened populations.

1 Introduction

Populations in nature are increasingly subjected to abrupt environmental changes, whether due to climate shifts, habitat alteration, or the introduction of new competitors [2, 4, 13]. These sudden disruptions can render previously well-adapted organisms maladapted, leading to declines in fitness and a heightened risk of extinction.

However, extinction is not always inevitable. In some cases, natural selection may act swiftly enough on standing genetic variation or new mutations to enable a population to adapt and persist, a process known as evolutionary rescue [6, 3, 11]. Understanding when and how this rescue occurs is a central question in evolutionary biology and conservation science. While answering this question can be approached from an ecological perspective, mathematical models also provide some insight; Gomulkiewicz and Holt [10] provide three mathematical models capturing various aspects of realism to analyze cases in which evolutionary rescue is possible.

However, the models proposed by Gomulkiewicz and Holt [10] do not account for various factors known to contribute to extinction, including climate change [20, 21, 5] and invasive species [12, 7, 16], as well as the loss of genetic diversity from population recovery [9, 1, 15]. As such, this study addresses a key question: Under what conditions can evolution actually rescue a population from extinction? To answer this, we explore both abiotic and biotic drivers of extinction, considering how the rate of environmental change, population genetic potential, and interspecific competition interact to determine the likelihood of survival. By expanding classical models of evolutionary rescue to incorporate gradual environmental change and biological invasions, we aim to better approximate the complexities of real-world ecosystems.

2 Methods

To investigate the impact of gradual environmental change on evolutionary rescue, we implemented and extended the three main models from Gomulkiewicz and Holt [10]: the two-step fitness model, the discrete-time quantitative genetic model, and the continuous-time diploid one-locus model. Each model implemented in the paper assumed an abrupt environmental change that caused an immediate reduction in fitness. We modified these models to better account for real-world factors leading to extinction, including simulating more realistic gradual environmental deterioration over time and simulating the interactions with an invasive species.

2.1 Brief Overview of Baseline Models

Gomulkiewicz and Holt [10] establish three baseline models to examine the cases in which evolution by natural selection can rescue a population from extinction. Specifically, they describe a simple two-step model, a quantitative genetic model, and a continuous time, one locus model. Here, we briefly outline the mathematics behind all models before addressing the additional changes we make to account for relevant extinction factors.

2.1.1 Two-Step Model

This model describes a population whose growth is determined by the following difference equation:

$$N_t = N_{t-1} \bar{W}_{t-1}$$

where \bar{W}_t is the mean relative fitness of the population at time step t . In the case where this is constant and less than 1, this population is doomed to extinction. However, by increasing this value by a constant selection factor s to simulate natural selection (i.e., $\bar{W}_t = \bar{W}_{t-1} + s$), populations can be rescued for certain parameter combinations. Note that for our simulations, population sizes were only tracked when they were less than the initial population size; this prevents a simulated explosion in populations, which allows for easier visualization of extinction recovery.

2.1.2 Quantitative Genetic Model

This model tracks a single trait with normally distributed phenotypes for a single population. At each time step, N_t phenotypes z for the population are sampled from $z \sim N(d_t, P)$. Each of these phenotypes has corresponding fitness $W(z) = W_{max} \exp[-z^2/2w]$, where W_{max} is the maximum fitness of any single phenotype and w corresponds to the width of the fitness curve; i.e., for larger w , more phenotypes will have higher fitness. This assumes that the optimal phenotype is always $z = 1$.

The model then calculates absolute mean fitness by the following integral:

$$\bar{W}_t = \int p_t(z) W(z) dz$$

where $p_t(z)$ is the probability of the corresponding phenotype. Alternatively, in the discrete case, this can be written as

$$\bar{W}_t = \frac{1}{N_t} \sum_{i=1}^{N_t} p_t(z) W(z).$$

The population after t time steps is then simply determined by $N_t = N_0 \prod_{i=1}^{t-1} \bar{W}_i$. Evolution is simulated by starting the initial d_t away from 0 and changing it every generation as

$$\Delta d_t = -\frac{h^2 d_t P}{P + w}$$

where h^2 is the narrow-sense heritability of the trait. In the event of successful evolution, d_t shifts towards 0, increasing the population's overall fitness.

2.1.3 Continuous-Time Diploid Locus Model

Since this model requires a diploid locus, this model must take the parameters of a fitness for each genotype. Gomulkiewicz and Holt [10] notate these fitnesses as m_{11} , m_{12} , and m_{22} . Then the mean fitness for the generation is simply defined as

$$\bar{m}_t = p_t^2 m_{11} + 2p_t q_t m_{12} + q_t^2 m_{22}.$$

Gomulkiewicz and Holt [10] utilize a continuous-time differential equation to then model the number of individuals, given as $\frac{dN}{dt} = \bar{m}N$. However, we approximate this continuous function with the forward Euler method, so $N_t = (1 + \bar{w})N_{t-1}$. While leaving this model in continuous form suited the original needs of Gomulkiewicz and Holt [10], our more complex versions require numerical analysis for simulations and solutions.

2.2 Gradual Climate Change Models

In the original two-step model, the population size is updated deterministically by multiplying by the fixed fitness parameter $w < 1$. If evolution was enabled, fitness increased linearly each generation by a selection coefficient s . In our gradual version, instead of constant fitness, w decreased linearly from w_{start} to w_{end} over a defined number of generations. Evolutionary rescue occurred if the population recovered above its initial size.

The original quantitative genetic model followed standard trait-based adaptation under stabilizing selection. In Gomulkiewicz and Holt [10], an abrupt shift in the optimal trait caused maladaptation, and the mean of the trait evolved each generation by a factor determined by heritability h^2 , variance P , and width of the fitness function w . In our gradual version, the environmental optimum shifted incrementally each generation. This allowed us to evaluate how continuous ecological change affects the population's ability to track the moving fitness peak.

The one-locus diploid model in the paper assumed a fixed genotype fitness determined by maximum fitness m_{max} and selection coefficient s . Fitness was calculated based on Hardy-Weinberg genotype frequencies. Our gradual extension simulated a fitness landscape that deteriorated over time, with m_{max} linearly decreasing between generations. This mimicked long-term habitat degradation, where optimal genotypes become less viable.

Simulations were run for 100 generations for the two-step and quantitative models and 40 generations for the one-locus model. We recorded population trajectories under various combinations of parameters to generate outcome grids that compare extinction, survival, and rescue in original and gradual models.

2.3 Invasive Species Models

Similarly, to understand the effect of interspecific competition on evolutionary rescue, we modified the baseline models to introduce an invasive species. In each model, we tracked the dynamics of a native population facing competition from an invasive species with a higher intrinsic fitness.

In our invasive-species version of the two-step model, rather than having constant fitness, the fitness of the native population n_t is reduced each generation by frequency-dependent competition from an invasive species a_t with higher intrinsic fitness, as given by the following system of equations:

$$\begin{aligned} n_t &= (W_{nt} - \beta_n \frac{a_{t-1}}{n_{t-1} + a_{t-1}}) * n_{t-1} \\ a_t &= (W_a - \beta_a \frac{n_{t-1}}{n_{t-1} + a_{t-1}}) * a_{t-1} \end{aligned}$$

This system assumes that the fitness of the invading species does not change over time. Furthermore, this system also introduces a parameter β , which indicates the impact of the other population's frequency on fitness. Evolutionary rescue similarly occurs if the native population recovers above its initial size despite competitive pressure.

In our invasive-species version of the quantitative genetic model, both the invading and the native population follow the same dynamics as the baseline model; however, we assume W_{max} for the invader is greater than W_{max} for the native; this reflects invasive species facing fewer threats in their novel environments. We also assume that P_a for the invader is less than P_n for the native; this reflects invasive species being introduced a few organisms at a time, implying less genetic diversity. Furthermore, the frequency-dependent effect on fitness from the two-step model is similarly applied in this model.

Finally, in our invasive-species version of the diploid locus model, competitive pressure from an invasive species altered the effective fitness of the native genotypes. Specifically, we assume that $w_{11,a} > w_{11,s}$; that is, the non-maladaptive genotype of the invader has higher fitness than the corresponding genotype of the native; furthermore, we assume $p_{0,a} < p_{0,n}$; that is, the invader has less maladaptation present than the invader.

2.4 Genetic Recovery Models

While not discussed in Gomulkiewicz and Holt [10], a pressing concern among conservation biologists is genetic diversity [8, 18]. Specifically, when a population attempts to rebound from a low population size, high levels of inbreeding can occur and lead to a loss in genetic diversity, making a recovered population susceptible to genetic diseases. So far, our extinction models have not taken this into account; as such, we introduce a model to track potential losses in genetic diversity.

For k single-nucleotide polymorphisms (SNPs) within a population, an individual’s genotype can be modeled as $x \in [0, 1]^{2 \times k}$, where each row represents the inherited paternal or maternal genetic material, each column a SNP, and 0 to represent the wild-type version of the SNP compared to 1 for the mutant version of the SNP. Our model starts by randomly assigning genotypes to n_{risk} individuals and gradually reproduces this population until a goal population size $n_{thriving}$.

To produce a new individual, two individuals are chosen at random from the current population, assigned to be the parents. To produce gametes from each parent, we start on the parent’s paternal or maternal row of its genotype at random, staying on the current row with probabilities according to given distances (in centiMorgans, cM) or given linkage disequilibria (LD). For simplicity, we assume that any distance $d < 50\text{cM}$ is converted to a probability $1 - (d/100)$ while any $d > 50\text{cM}$ is set to 0.5, and any LD $r^2 < 0.5$ is set to probability 0.5, while any $r^2 > 0.5$ is directly used as a probability. While this simplicity does not capture the full nuances of linkage disequilibrium, it allows for ease of modeling.

For example, suppose we are given the genotype $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$. To start the paternal or maternal genotype of the offspring, we chose from column 1, row 1 or 2 with probabilities 0.5. Then, if we establish that the distance between SNPs 1 and 2 is 40 cM, or that these two SNPs have an LD of $r^2 = 0.6$, the probability of staying on the same row as when we started is 0.6. As such, the gametes in this example are (1, 0), (0, 1), (1, 1), and (0, 0) with produced with respective probabilities 0.3, 0.3, 0.2, and 0.2.

We simulated genetic recoveries using this framework, in addition to the assumption that for n_t individuals at generation t , all individuals at generation $t + 1$ are offspring of the previous generation; that is, we assume that individuals live only one generation and reproduce for the next. Furthermore, we assume that generation $t + 1$ has $n_t + 1$ individuals; that is, only one new individual is produced each generation. This is often reflective of low reproduction rates in many endangered species, especially large mammals such as elephants and cetaceans.

3 Results

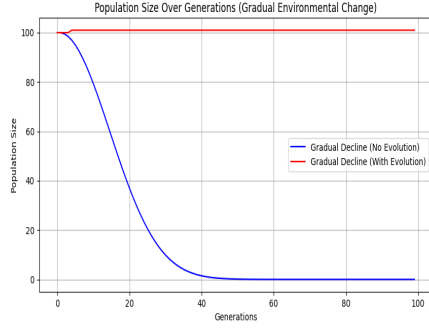
3.1 Gradual Climate Change Models

Across all three models, the introduction of gradual environmental change significantly altered the likelihood of evolutionary rescue.

In the two-step model, populations with initially moderate fitness ($w_{start} = 0.95$) declined rapidly under abrupt change unless paired with strong evolutionary recovery 1a. However, in gradual decline, even small selection coefficients ($s = 0.01$) were sufficient to prevent extinction, allowing the population to stabilize or recover fully. Rescue occurred more frequently in this setting, as shown by the expanded survival region in the parameter (Figure 1b).

In the quantitative genetic model, gradual environmental changes allowed populations to better track the changing optimum. Under abrupt change, only populations with high heritability ($h^2 \geq 0.8$) and low variance could survive (Figure 2). Gradual change extended survival to populations with moderate heritability and higher variance. The single simulation trajectory (Fig. 2a) shows that the gradual movement of the optimum trait enables populations to maintain viable sizes longer compared to abrupt shifts. The visualization of the grid (Figure 2b) shows a broader range of combinations that produce persistence and delayed population collapse. However, survival still required some minimum level of adaptive capacity, for example, populations with low h^2 and high P still failed to adapt.

The one-locus model revealed the least sensitivity to gradual change. In Gomulkiewicz and Holt [10], populations with high initial maladaptation (high q_0) and low selection pressure quickly went

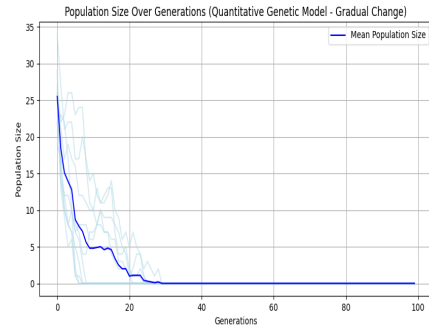


(a) Population trajectories for the two-step model under gradual decline. The blue curve shows decline without evolution ($s = 0$), while the red curve shows population rescue with a small selection coefficient ($s = 0.01$).

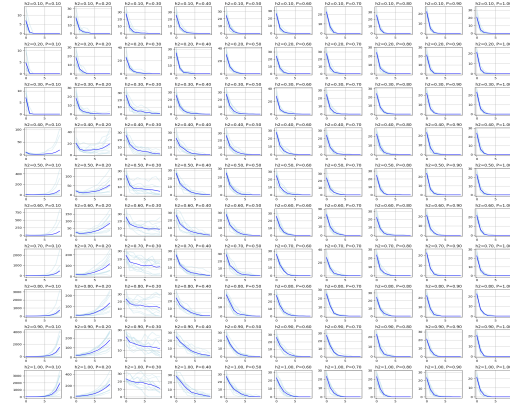


(b) Grid of simulations from the gradual two-step model varying w_{start} and s . Blue curves show recovery; white regions indicate extinction. Gradual decline and small s values enable rescue where baseline models would fail.

Figure 1: Two-Step Model under gradual environmental change.



(a) Mean population size over 10 replicate simulations of the gradual quantitative genetic model. Individual trajectories (light blue) show variation; the dark blue curve shows the mean trend toward extinction or survival.

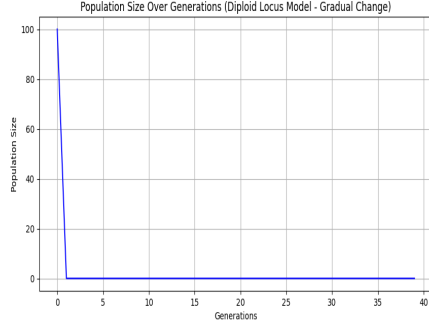


(b) Grid of simulation outcomes for the gradual quantitative genetic model across varying h^2 and phenotypic variance P . Survival is expanded at intermediate h^2 compared to abrupt change.

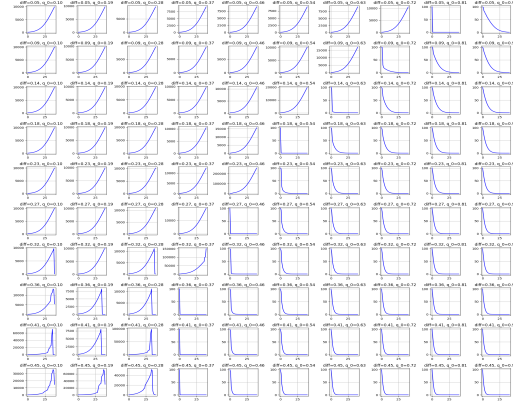
Figure 2: Quantitative Genetic Model under gradual environmental change.

to extinction. With gradual decline in m_{max} , extinction was delayed but often still inevitable unless s was large and q_0 was relatively low. The single trajectory (Fig. 3a) illustrates that even gradual deterioration, the population size eventually drops below viable levels. The grid results (3b) showed some new combinations that allowed temporary persistence, but ultimate recovery remained rare.

Collectively, these results support the idea that gradual environmental change increases the likelihood of evolutionary rescue. The effect was strongest in the two-step model and quantitative genetic models, where adaptation could respond meaningfully to a slowly shifting environment. In contrast, the one-locus model showed limited gains, suggesting the genetic architecture and environmental environment. pacing interact to determine the probability of persistence.



(a) Population trajectory for a single simulation of the gradual one-locus model. Even with slower environmental decline, extinction occurs after an extended low-population phase.



(b) Grid of outcomes for the gradual one-locus model across different initial maladaptations q_0 and selection differentials $s - m_{\max}$. Temporary persistence observed in limited cases, but extinction remains frequent.

Figure 3: One-Locus Model under gradual environmental change.

3.2 Invasive Species Models

3.2.1 Two-Step Model

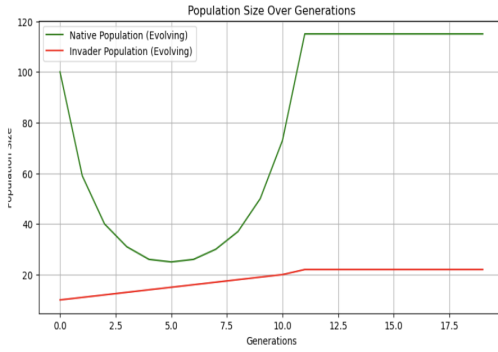
The introduction of an invasive species significantly increased the extinction risk for the native population in the two-step model. In the absence of evolution, native populations declined rapidly following competition with invaders of higher intrinsic fitness. However, when evolution was enabled, native populations could sometimes recover by gradually increasing their fitness over generations, as seen in the trajectory plot (Figure 4a).

Outcome grids across varying initial native fitness w and selection coefficients s revealed that evolutionary rescue was possible only within a narrow range of parameters (Figure 4b). Specifically, successful rescue required both a sufficiently high initial native fitness and moderate evolutionary response rates. Without sufficient selection pressure, the native population consistently went extinct even if the initial fitness was relatively high. The presence of invasive species shifted the survival threshold upwards, making evolutionary rescue harder compared to baseline models without competition.

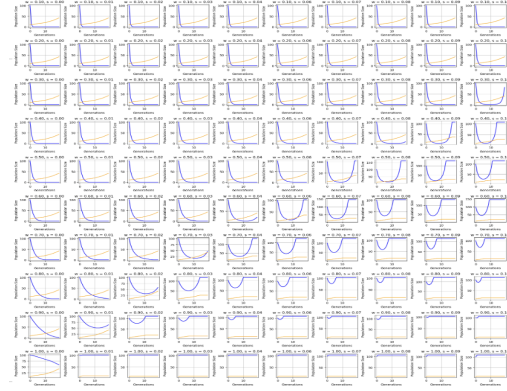
3.2.2 Quantitative Genetic Model

In the quantitative genetic model, competition from an invasive species dramatically limited the native population's ability to track the optimal trait. Without evolution, native populations declined rapidly after the introduction of the invader. Even with evolutionary adaptation, native populations often failed to recover unless they had both high heritability (h^2) and low phenotypic variance (P), as shown in Figure 5a.

Outcome grids across varying h^2 and P values revealed that evolutionary rescue was much more restricted under invasive pressure compared to the baseline case (Figure 5b). Populations required very high heritability and low phenotypic variance to survive competition. Most parameter combinations led to either rapid extinction or only brief persistence before collapse. The competitive advantage of the invasive species shifted the survival boundaries, highlighting the strong constraining effect of biotic stress on evolutionary rescue.

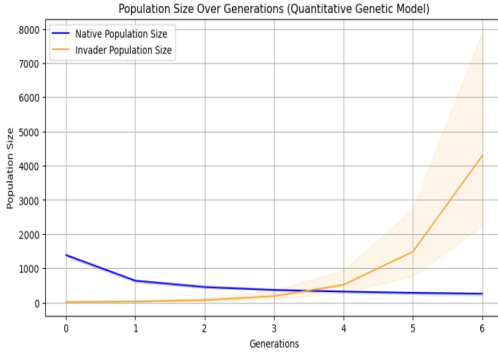


(a) Population trajectories for the two-step model with an invasive species under different evolutionary scenarios.

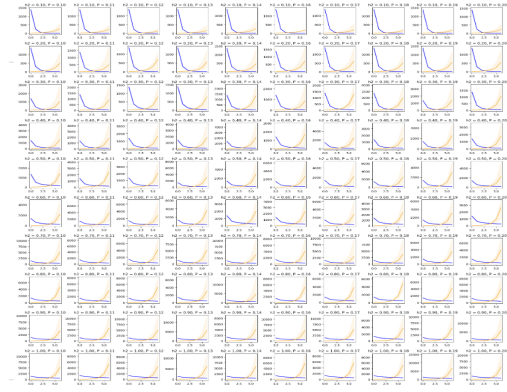


(b) Grid of simulation outcomes varying initial fitness w and selection coefficient s under invasive competition.

Figure 4: Two-Step Model with invasive species. The presence of an invader raises the threshold for evolutionary rescue, making native persistence more difficult.



(a) Population trajectories for the quantitative genetic model with an invasive species under different evolutionary scenarios.



(b) Grid of simulation outcomes varying h^2 and P under invasive competition.

Figure 5: Quantitative Genetic Model with invasive species. Invasive competition narrows the conditions under which evolutionary rescue is possible.

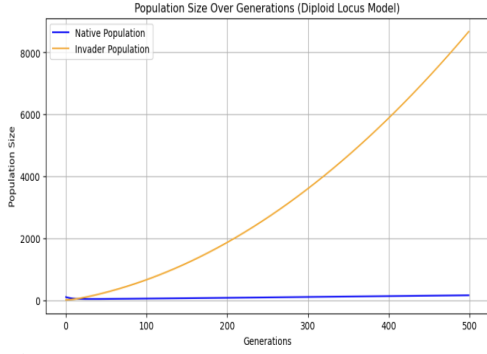
3.2.3 Diploid One-Locus Model

The one-locus diploid model showed the lowest potential for evolutionary rescue under invasive competition. In nearly all parameter settings, the native population failed to recover, even when evolutionary processes were active. The invasive species' competitive advantage consistently suppressed the native population, resulting in flat or declining trajectories (Figure 6a).

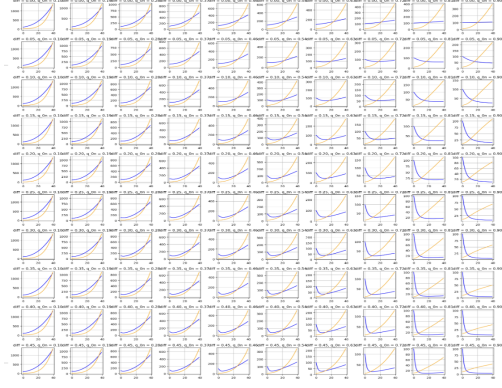
Grid outcomes across combinations of initial maladaptation (q_0) and selection differential ($s - m_{\max}$) showed that evolutionary rescue occurred in only a few rare parameter regimes (Figure 6b). Temporary persistence was occasionally observed when initial maladaptation was low and selection differential was high, but most simulations still ended in extinction. These results highlight the sensitivity of evolutionary rescue to genotype structure and the powerful constraints imposed by invasive competitors.

3.3 Genetic Recovery Models

Across 100 SNPs for an increase in population from 10 to 100 individuals, we found a significant loss in genetic diversity; a large portion of the SNPs became population-homogeneous with a wild-type or



(a) Population trajectories for the diploid one-locus model with an invasive species. Native populations show limited recovery even under evolution.



(b) Grid of outcomes across initial maladaptation q_0 and selection differentials $s - m_{\max}$. Temporary persistence is rare and rescue remains limited.

Figure 6: Diploid One-Locus Model with invasive species. Competitive pressure from the invader limits the parameter space for successful evolutionary rescue.

mutant allele frequency of 0 or 1 (Figure 7). Across 10 simulations, we found an average of 26.9 out of the 100 SNPs became population-homogeneous.

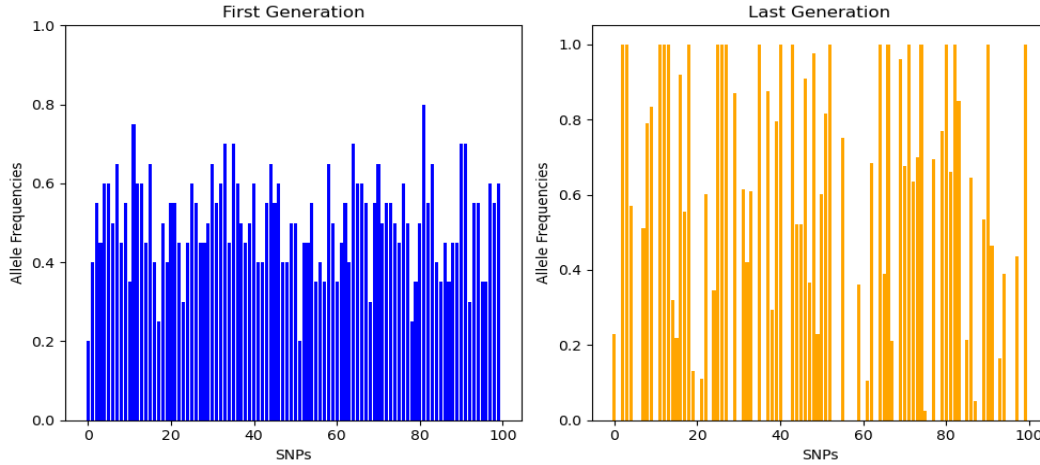


Figure 7: Allele frequencies of the wild-type allele across 100 SNPs tracked across a genetic recovery simulation for the first generation (left) and last generation (right).

4 Discussion

Our simulations reveal that gradual environmental change, while not eliminating the possibility of extinction, significantly broadens the conditions under which evolutionary rescue can occur. In contrast to abrupt shifts, gradual change allows more time for adaptive evolution to counteract population decline. This extended window increases the likelihood of recovery for populations with moderate evolutionary potential, those that would otherwise fail to adapt quickly enough under sudden stress. Importantly, gradual change shifts the threshold between extinction and survival, enabling evolutionary rescue across a wider range of parameter combinations, especially where adaptation was previously too slow to prevent collapse.

We introduced gradual change to better reflect real-world scenarios where extinction risk arises not only from abiotic factors but also from biotic pressures. In particular, invasive species are a major driver of biodiversity loss across ecosystems. Classic examples include the introduction of rats and

mongooses in Hawaii [14], which devastated native bird populations. To model this, we incorporated a competing invasive species whose fitness decreases with its own density, while the native species benefits from positive frequency dependence, a proxy for social or cooperative advantages. Crucially, the invader has a higher maximum fitness, simulating the asymmetry often observed in real-world invasions.

Our results also show that invasive species consistently increase extinction risk. This finding, while intuitive, is quantitatively supported by our simulations: in no instance does the presence of an invasive species reduce the threat of extinction for the native population. Rather, invaders either extend the period during which the native population remains below a critical density or entirely prevent its recovery. This underscores the severity of biotic threats and the challenges they pose to evolutionary rescue.

Furthermore, our results indicate that even in cases where a population is able to rebound and grow to a thriving size, it often comes at the loss of tremendous genetic diversity, where around a quarter of simulated SNPs became population-homogeneous. This loss of genetic diversity can put a vulnerable population at greater risk for disease [19, 17], reducing fitness and potentially adding more complications to rescue from extinction.

The potential for evolutionary rescue is governed by several interacting factors: the rate of environmental change, the size and genetic variability of the population, and the strength of stabilizing selection. Gradual environmental shifts, unlike abrupt shocks, provide populations a better chance to track the moving optimum through adaptation. However, this potential is significantly constrained by the presence of invasive species, which elevate competitive pressure and reduce the adaptive space available for native species. This potential can be further constrained by the loss of genetic diversity in a population's attempt to rebound in size; the specific impact of genetic diversity loss thus forms a natural next direction for future research.

This project directly aligns with the core themes of the Modeling Evolution course by integrating mathematical modeling with evolutionary theory to explore population persistence under changing environments. We used simulation-based approaches to study how selection and mutation interact to shape evolutionary rescue dynamics. This work reflects the course's emphasis on using quantitative tools to understand evolution as a dynamic, context-dependent process, and it deepens our grasp of how theoretical models can inform conservation strategies in the face of ecological threats like climate change and species invasions.

By developing and analyzing these models, we also gained experience with core tools of population genetics, reinforcing the course's goal of using simple, idealized models to build intuition about complex evolutionary systems. Overall, this project provided a concrete opportunity to apply theoretical principles to open questions in evolutionary biology.

Our simulations share a deep connection with conservation biology. Many threatened species persist in small, fragmented populations due to habitat loss, deforestation, or climate change. These populations may face compounded risks from both environmental stress and biological invasions. An important avenue for future work is to determine whether evolutionary rescue is still feasible under reduced carrying capacities. Smaller populations experience greater fitness stochasticity and diminished genetic input per generation, slowing the pace of adaptation and narrowing the critical time window for rescue.

Future studies should focus on identifying minimum viable population sizes that enable rescue in gradually changing environments. Additionally, integrating landscape-scale heterogeneity and migration could provide deeper insights into metapopulation dynamics under invasion and environmental change.

Code Availability

All code is available at <https://github.com/jonazhu/extinctionmodeling>.

References

- [1] Morten E Allentoft and John O'Brien. Global amphibian declines, loss of genetic diversity and fitness: a review. *Diversity*, 2(1):47–71, 2010.

- [2] Richard B Alley, Jochem Marotzke, William D Nordhaus, Jonathan T Overpeck, Dorothy M Peteet, Roger A Pielke Jr, Raymond T Pierrehumbert, Peter B Rhines, Thomas F Stocker, Lynne D Talley, et al. Abrupt climate change. *science*, 299(5615):2005–2010, 2003.
- [3] Graham Bell and Andrew Gonzalez. Evolutionary rescue can prevent extinction following environmental change. *Ecology letters*, 12(9):942–948, 2009.
- [4] Filippo Botta, Dorte Dahl-Jensen, Carsten Rahbek, Anders Svensson, and David Nogués-Bravo. Abrupt change in climate and biotic systems. *Current Biology*, 29(19):R1045–R1054, 2019.
- [5] Abigail E Cahill, Matthew E Aiello-Lammens, M Caitlin Fisher-Reid, Xia Hua, Caitlin J Karanewsky, Hae Yeong Ryu, Gena C Sbeglia, Fabrizio Spagnolo, John B Waldron, Omar Warsi, et al. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280(1750):20121890, 2013.
- [6] Stephanie M Carlson, Curry J Cunningham, and Peter AH Westley. Evolutionary rescue in a changing world. *Trends in ecology & evolution*, 29(9):521–530, 2014.
- [7] Miguel Clavero and Emili García-Berthou. Invasive species are a leading cause of animal extinctions. 2005.
- [8] J Andrew DeWoody, Avril M Harder, Samarth Mathur, and Janna R Willoughby. The long-standing significance of genetic diversity in conservation. *Molecular ecology*, 30(17):4147–4154, 2021.
- [9] Alisse Garner, Janet L Rachlow, and Jason F Hicks. Patterns of genetic diversity and its loss in mammalian populations. *Conservation Biology*, 19(4):1215–1221, 2005.
- [10] Richard Gomulkiewicz and Robert D Holt. When does evolution by natural selection prevent extinction? *Evolution*, pages 201–207, 1995.
- [11] Andrew Gonzalez, Ophélie Ronce, Regis Ferriere, and Michael E Hochberg. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution, 2013.
- [12] Jessica Gurevitch and Dianna K Padilla. Are invasive species a major cause of extinctions? *Trends in ecology & evolution*, 19(9):470–474, 2004.
- [13] Hervé Guyard, Emmanuel Chapron, Guillaume St-Onge, Flavio S Anselmetti, Fabien Arnaud, Olivier Magand, Pierre Francus, and Marie-Antoinette Mélières. High-altitude varve records of abrupt environmental changes and mining activity over the last 4000 years in the western french alps (lake bramant, grandes rouses massif). *quaternary science reviews*, 26(19-21):2644–2660, 2007.
- [14] Cheryl A Lohr and Christopher A Lepczyk. The impacts of introduced mammals in the hawaiian islands: a literature review. In *Proceedings of the Vertebrate Pest Conference*, volume 24, 2010.
- [15] Margaret E Montgomery, Lynn M Woodworth, Roderick K Nurthen, Dean M Gilligan, David A Briscoe, and Richard Frankham. Relationships between population size and loss of genetic diversity: comparisons of experimental results with theoretical predictions. *Conservation Genetics*, 1:33–43, 2000.
- [16] Harold A Mooney and Elsa E Cleland. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10):5446–5451, 2001.
- [17] Stephen J O’Brien and James F Evermann. Interactive influence of infectious disease and genetic diversity in natural populations. *Trends in Ecology & Evolution*, 3(10):254–259, 1988.
- [18] David H Reed and Richard Frankham. Correlation between fitness and genetic diversity. *Conservation biology*, 17(1):230–237, 2003.
- [19] Derek Spielman, Barry W Brook, David A Briscoe, and Richard Frankham. Does inbreeding and loss of genetic diversity decrease disease resistance? *Conservation Genetics*, 5:439–448, 2004.

- [20] Chris D Thomas, Alison Cameron, Rhys E Green, Michel Bakkenes, Linda J Beaumont, Yvonne C Collingham, Barend FN Erasmus, Marinez Ferreira De Siqueira, Alan Grainger, Lee Hannah, et al. Extinction risk from climate change. *Nature*, 427(6970):145–148, 2004.
- [21] Mark C Urban. Accelerating extinction risk from climate change. *Science*, 348(6234):571–573, 2015.