

Evolutionary Rescue in Conservation: A Theoretical Model inspired by the Iberian Lynx (*Lynx pardus*)

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Abstract

Conservation efforts often focus on immediate interventions such as habitat restoration or ex situ breeding programs to prevent extinction. However, populations may also recover through evolutionary rescue – a process where adaptive genotypes spread rapidly enough to restore population growth before extinction occurs. This model explores the potential for evolutionary rescue in *Lynx pardus*, inspired by the real-world recovery example of this Lynx species. Using a stochastic, discrete-time simulation approach incorporating distinct environmental noise and fitness effects, density dependence and allee-effects, I investigated how the introduction of a defined number of genetically distinct individuals affects population rescue and survival. Populations were simulated under haploid and diploid, or more precisely, under panmictic and non-panmictic conditions, with distinct fitness and environmental sensitivities for wildtype, mutant (and heterozygous) genotypes.

Results show that without reintroduction rescue, wildtype populations with lower fitness are in serious risk and prone to extinction, even under moderate or low environmental variability. Introducing fitter “mutant” individuals can trigger autonomous recovery through evolutionary rescue, provided a critical release fraction is exceeded. Simulations in the given framework resulted in the suggestion that a minimum of approximately 25 fitter individuals, relative to the depleted wild population consisting of 100 wild type individuals, is required to achieve the target value of 80% probability of rescue. These findings emphasize that genetic and demographic parameters strongly influence recovery thresholds and highlight the potential of evolutionary processes to complement classical, conventional strategies used in recent conservation.

1. Introduction

Conservational rescue often focuses on populations that are doomed for extinction. Loss of habitat and the resulting fragmentation, poaching and many other factors often lead to decreasing populations and loss of biodiversity. Conservation measures often focus on habitat restoration, legislation regulations and conducting ex situ breeding programs, creating reserve populations and being able to regularly reinforce populations with reintroduction programs. This often includes reintroduction of species in habitats where they have already been lost, for example Eurasian lynx in Switzerland. Previous work in theoretical ecology modeled reintroductions of lost predators and the results imply that trophic cascades undergo significant changes, and reintroductions of lost predators sometimes have consequences we did not consider in conservation to this day. Results of said modeling implies that such reintroductions may cause secondary extinction events due to changes in trophic cascades since eradication of the species to rescue, being dangerous to ecosystems in the affected habitats and bearing serious possible risks of losing biodiversity because of rescue and reintroduction. Repopulation projects in conservation are also often very extensive in research, surveillance and maintenance, programs often requiring extensive ex situ breeding programs and repeated, regular releases of individuals from reserve populations to rapidly reinforce populations to sustainable numbers. The following theoretical rescue model is inspired by the real world conservation example of the Iberian Lynx (*Lynx pardus*).

This lynx species is endemic to the Iberian peninsula, being part of the top of the foodchain in its respective ecosystems (among others). As an apex predator, Iberian lynx take a crucial role in the endemic trophic cascade in keeping the ecosystems at equilibrium. Loss of this predator would bear serious, irreversible biodiversity consequences. In the early 2000s, population of lynx *pardus* were as low as less than 100 individuals. The endemic flagship species of Iberia was at serious risk of going extinct. Conservationists were very engaged in doing everything it takes to rescue this species. A conservation plan was called into life, including capturing wild individuals to breed individuals in ex situ programs. The plan also included annual releases of bred individuals into the wild.

As soon as a species is in serious danger of going extinct, conservationists assist populations in every possible way to ensure populations grow as fast as possible. Sometimes we tend to forget how natural systems, in its own ways, show remarkable sophistication when it comes to keeping up its balance and being very persistent. We always tend to think of ecosystems or species as being very fragile and in need of extensive husbandry to maintain homeostasis. But what if, given that anthropogenic interventions more often than not, lead to disturbance and sometimes irreversible effects in ecosystems, trophic cascades and overall equilibrium, we overthink the trivial and conventional approaches in conservation as to limiting direct conservational intervention for species to a minimum? Inspired by this question, in regards of

evolutionary rescue, the following theoretical model emerged. The key question amounts to how evolutionary rescue could have acted in rescue of the Iberian lynx population in this case. Considering vastly declined populations suffering from homozygosity, limited geneflows due to fragmentation, inbreeding depressions, and thus negative fitness effects, under the assumption that environmental fluctuations also affect population dynamics, how might such populations have been able to rescue itself, if individuals with different, more advantageous genotypes bred in captivity got introduced to the declining wildtype population?

The idea of this model is that reintroducing individuals with distinctive genotypes and fitness levels happens only one time, when the population has reached its floor. The questions this model tries to investigate is

- a) What are possible population scenarios after introducing certain mutant fractions into the wild
- b) What is the minimal release fraction of said individuals so the population is able to recover without further intervention, driven by resulting evolutionary rescue?
- c) Under what circumstances is the population able to recover given the model parameters and framework

2. Model & Methods

2.1. The model:

Parameters and Values:

N_a:	Wildtype Population	dens:	Density dependence on total pop.	r_a/r_A:	Expected mean population growth for A and a («Lambda»)
N_A:	Mutant Population	allee:	Allee-Effect on total pop.	A:	Allee-parameter
N_tot:	Total Population: $N_a + N_A$	sigma_env:	SD of normal distribution of environmental stochasticity function	K:	Population Carrying-Capacity
w_a/w_A:	Intrinsic fitness values for WT and Mutant	env:	Environmental stochasticity: drawn from normal distribution	max_gen:	Number of maximum generations per simulation

The model assumes distinct intrinsic fitness values for each genotypes, wildtype and “mutants” (referring to captivity-bred individuals for rescue).

The model further takes environmental fluctuations into account, affecting both types differently. While mutants generally bear higher fitness, they are more strongly affected by environmental stochasticity. We can imagine this as mutants being bred in captive programs, they are less adapted to the wild environment. Iberian lynx mainly depend on rabbits as main nutrition source. When rabbit populations are abundant, the mutants are able to thrive better due to their fitness advantage. When prey is scarce, they are less able to handle the adversity due to hunting skills being less adapted compared to their wild raised counterparts. This and other effects lead to the mutants being more vulnerable to the whim of nature.

The population underlies logistic density dependent growth, as well as allee effects, meaning populations in lower densities have lower growth rates which seems biologically reasonable.

2.2. Defining growth functions and Simulation of first, non-panmictic generation

In a first step, we simulate the first generation of a non-panmictic, haploid, non-mutating population after introducing a given number of mutant individuals (A) for rescue, drawing the next generation from a poisson distribution of expected growth under environmental stochasticity:

$$N_a(t_1) \sim \text{Poisson}(r_a \cdot \text{env} \cdot N_a)$$

Expected population growth rate r results from the intrinsic fitness (w) multiplied with density dependence and a weakened Allee-value:

$$r_a = w_a \left(1 - \frac{N_{tot}}{K}\right) \left(\frac{N_{tot}}{N_{tot} + A}\right)^{0.5}$$

Total population results from Wildtype population and Mutant Population:

$$N_{tot} = N_a + N_A$$

For environmental noise, we draw a value from a normal distribution in each generation:

$$\text{env} \sim \mathcal{N}(\mu = 1, \sigma = "sigma_env")$$

where the parameter “sigma_env” represents the standard deviation in environment conditions, while the mean value is 1, meaning that, on average, across the time frame of all simulations, the environment is at equilibrium and is neutral in terms of fitness affect in lynx.

2.3. Simulation of non-panmictic population

In a next step, we simulate a singular outcome of population rescue across 100 generations. Simulation breaks if population drops to zero (extinction):

Insert table here

2.4. Extinction probabilities without rescue

Next, we are plotting the extinction probability without rescue under varying environmental stochasticity:

insert figure here

And under varying intrinsic wildtype fitness, with fixed environmental stochasticity:

insert figure here

2.5. Simulating the population as panmictic with diploid loci

The previous simulation gives us the results for a non-panmictic population with haploid loci. Now we want to make the population and the mutation locus diploid and panmictic and investigate rescue under these biologically more accurate circumstances. For the following step, we're going to use the Hardy-Weinberg equation.

For this step, we define Parameters and values for the heterozygote genotype (Aa):

w_Aa	Heterozygote intrinsic fitness parameter
sig_Aa	SD value for heterozygote environmental noise effect
r_Aa	Expected growth rate for heterozygote

All parameters and variables are calculated and defined the same way as in our non-panmictic population. Additionally, we need to count the diploid allele frequencies for every generation step as follows:

$$A = 2N_{AA} + N_{Aa}$$

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Next, we calculate Allele frequencies under Hardy-Weinberg conditions:

$$p_A = \frac{A}{2N_{tot}}, p_a = \frac{a}{2N_{tot}}$$

Finally, we calculate the Hardy-Weinberg genotype frequencies:

$$p_{AA} = p_A^2, p_{Aa} = 2p_A p_a, p_{aa} = p_a^2$$

We draw random offspring via “rmultinom” for the next generation and simulate the diploid population over 100 generations as in the previous simulation.

The previous simulation models possible population outcomes for mutations which are homozygous and codominant. Given codominance of the loci, we assign intrinsic fitness parameter and environmental stochasticity effect on population growth (sigma_env), which lie in between the values for homozygous mutant and wildtype.

But what if we want model the mutation to occur on a single locus and being dominant compared to wildtype fitness?

2.6. Modeling the population for a single locus heterozygous mutation

It is not necessary to change the model, it is sufficient to only adjust a few parameters. For instance, we remove fitness and environmental effect for the Homozygous Mutant (AA). This consequently means that homozygous and heterozygous mutants have the same fitness and are equally prone to environmental effects. Change in initial population sizes change to zero AA types and the fraction of reintroduced mutant individuals switching genotype (now Aa). We also simulate this scenario to investigate if there are differences in terms of population composition.

2.7. Calculating minimal release number for $\geq 90\%$ rescue probability

In the last step, we want to investigate the minimum number of introduced mutant individuals to rescue the declining wildtype population at N=100. Rescue probability needs to be at least 90% across 1000 simulations ($p \geq 0.90$). Population is considered extinct if at any point in a single simulation the total population drops to zero ($N = 0$). The population is considered “rescued” if after t_{max} generations, the total population size exceeds 500 individuals, which we consider a stable population size able to self sustain.

insert sketch and/or table explaining the model or potential model outcomes

3. Results

3.1. Simulating the first generation; Na=100, NA=20

Coding a single run of the first generation outcome after introduction gave new population size of 74 Wild type (aa) and 17 mutant (AA) individuals, with new total population (N) changing from 120 to 91 individuals:

```
> simulate_one_gen1 <- function(N_a, N_A, w_a, w_A, R_rate, sigma_en  
v_a, sigma_env_A, K, A)  
  
> print(simulate_one_gen1(100,20,1.01,1.2,0, sigma_env_a = 0.1,  
sigma_env_A = 0.3, K=5000, A=20))  
[1] 74 17
```

3.2. simulating the non-panmictic population

The following figures illustrate plots, providing (possible) single simulation outcomes for wildtype populations (aa) of $N=100$, with varying mutant (AA) introduction numbers:

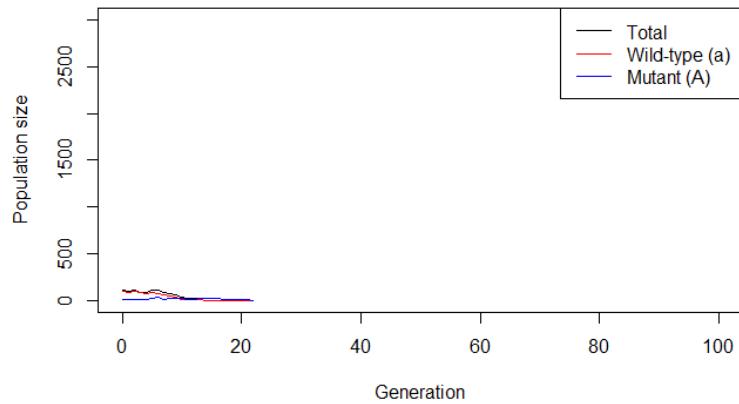


Figure 1: Non-panmictic Population trajectory for $N(A)=10$ resulting in extinction

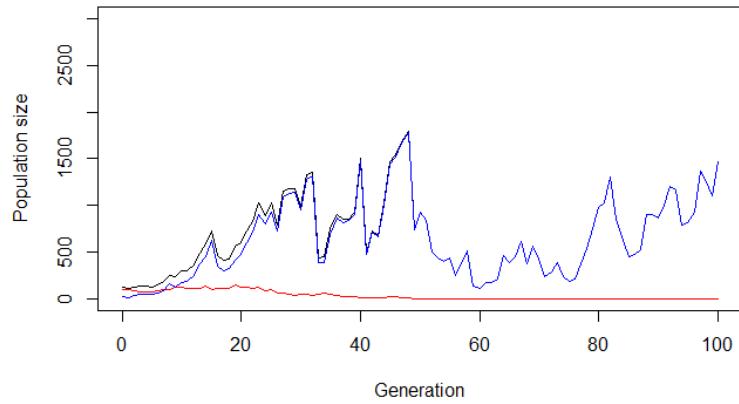


Figure 2: Non-panmictic population trajectory for $N(A)=20$ resulting in rescue

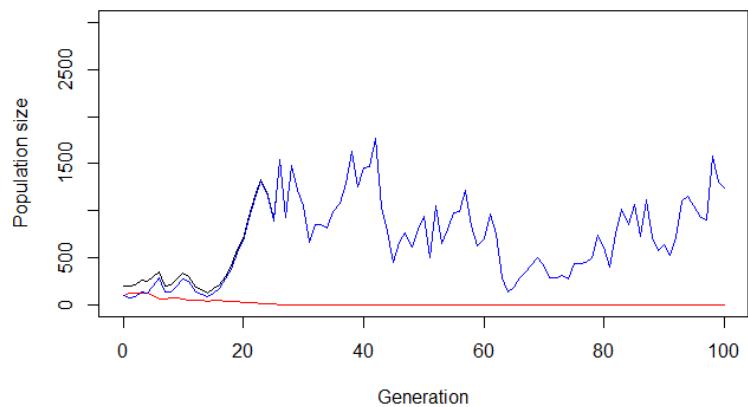


Figure 3: Non-pandemic population trajectory for $N(A)=100$ resulting in rescue

3.3. extinction probabilities without rescue

The figures in this section show simulation outcomes for varying environmental stochasticity (σ_{env}) and varying intrinsic wildtype fitness values (w_a), given the circumstance of no intervention or rescue by mutants:

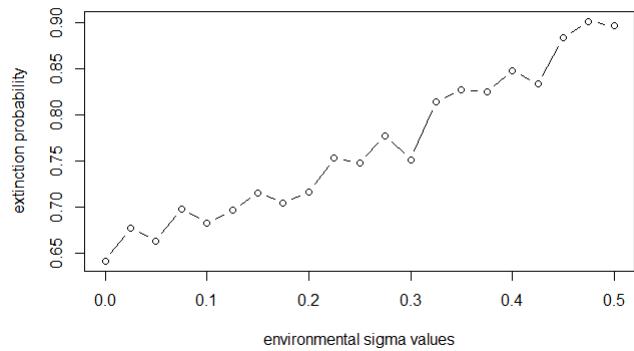


Figure 4: Extinction probability under varying environmental stochasticity

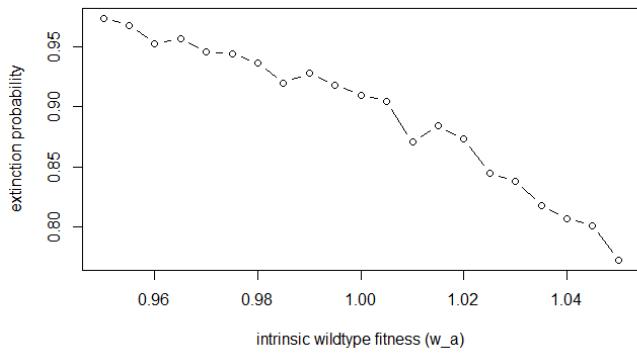


Figure 5: Extinction probability under varying intrinsic fitness values

3.4. simulating diploid panmictic population

As in the first simulation with non-panmictic populations, we simulate the first generation after mutant introduction:

```
> simulation_diploid <- function(N_aa, N_Aa, N_AA, w_a, w_Aa, w_A, R_rate,
+ sigma_env_a, sigma_env_A, sigma_env_Aa, K, A)

> simulation_diploid(100, 0, 20, 1.1, 1.2, 1.3, 0, 300, 0.1 ,0.3, 0.2,
5000, 20)

pAA pAa paa
 3   40   91
```

Simulation of population over 100 generations:

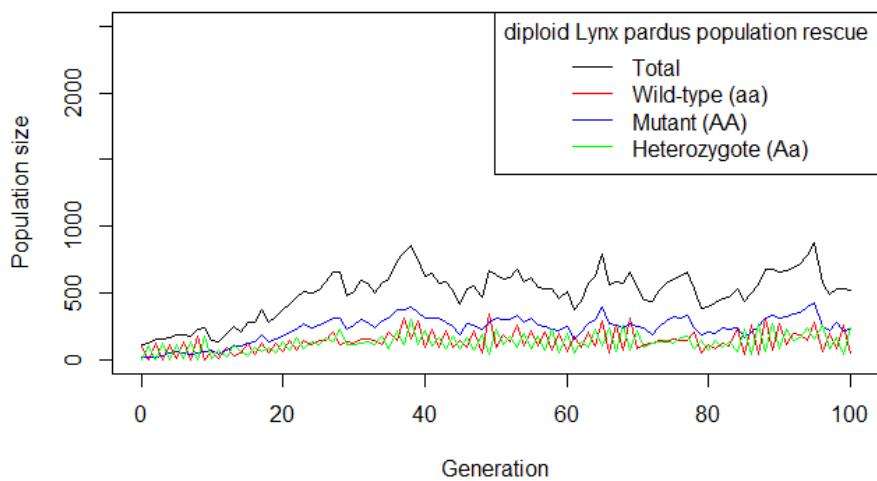


Figure 6: Diploid Population trajectory for $N(AA)=20$ resulting in rescue

3.5. single-locus heterozygous mutation :

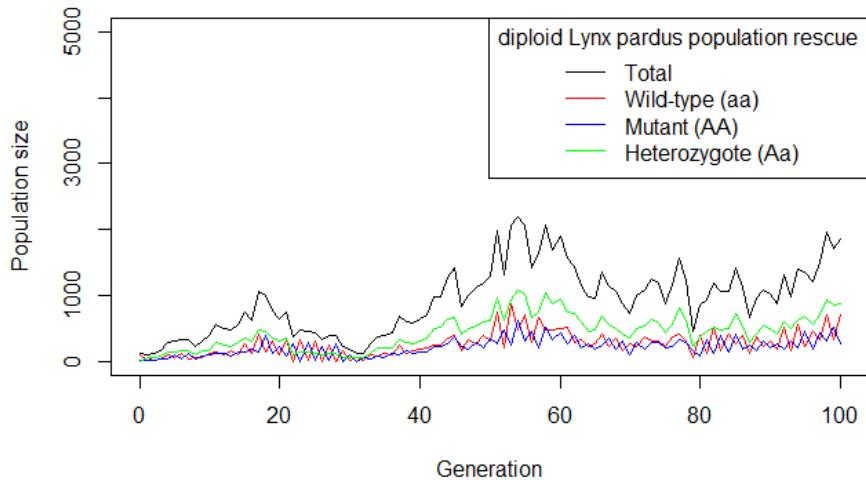


Figure 7: Diploid population trajectory for $N(Aa)=20$ resulting in rescue

3.6. calculating minimal release numbers

The following plot (Figure 8) shows population rescue probability, given varying introduction fractions (relative to wildtype population of $N=100$) of Mutant individuals (AA or Aa), highlighting the range of target rescue probability of $p \geq 0.8$:

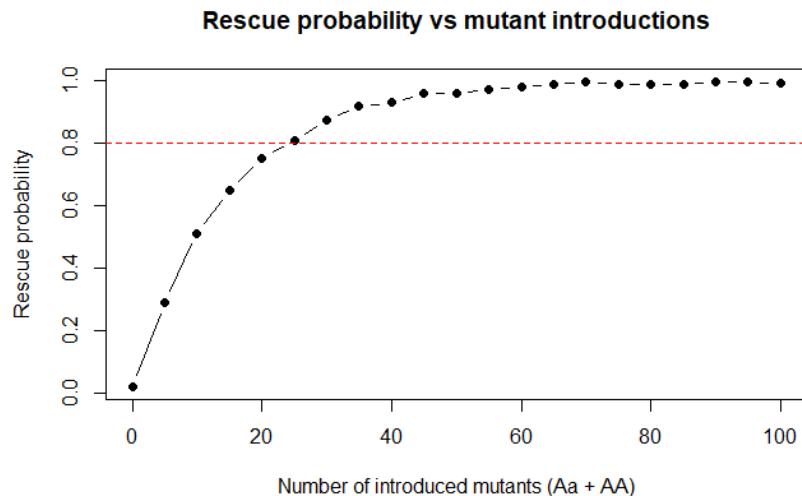


Figure 8: Rescue Probability for number of introduced individuals

4. Discussion

Throughout the different non-panmictic population simulations we can observe that the wildtype in most cases is due to go extinct if populations of wildtype and mutant do not overlap. For small release sizes (Figure 1) we see that the population is not able to recover and goes extinct, indicating that for small release sizes, the chance of recovery is low, although the population manages to retain for a few generations.

Figure 2 shows steady growth in the beginning, with the initial wildtype population even being able to increase under the new company of introduced mutant types, but after a few generations it gets outcompeted and ceases to exist. The mutation type takes over the entire population, but is able to increase and eventually achieving a stable state.

Figure 3 showcases an extreme case of 100 individuals of the mutant type being introduced into the population, thus making the ratio of phenotypes 1:1. We observe a strikingly similar pattern to Figure 2 ($NA=20$), with wildtypes even increasing at the beginning and mutants showing a slight decrease, but wildtype eventually gets outcompeted once again, this time the process being much more accelerated. This implies that in the long term, populations experience a similar outcome in rescue and oscillations, with release fractions only affecting the population in the short term outcome and accelerated recovery.

Simultaneously we wanted to investigate how different magnitudes of annual environmental fluctuations, and differences in intrinsic wildtype fitness affect extinction probabilities of the wildtype population of N=100, respectively, given that no reintroduction or conservational intervention occurs. Interestingly, we observed correlations for both variables. For environmental sigma value (SD), we investigated values between 0.0 and 0.5, sequenced the range in 20 parameter values. For fitness, we investigated values from 0.95 and 1.05 and sequenced the range into 50 parameter values, and running 1000 simulations for each parameter value in both parameters. The results show that small deviations in intrinsic fitness, as well as magnitude of environment changes can bear significant effects on population extinctions.

Logically, the next step in population modeling was to make the loci diploid and the population panmictic, allowing for heterozygotes and genetic reassorting.

Now the question is whether the mutations are dominant and heterozygous or homozygous and codominant with the wildtype and whether it affects the population outcome after introduction and to what extent. Population dynamics differ quite much in both scenarios. Seemingly, total population reaches higher peaks when introduced mutants are heterozygous (Figure 7). Heterozygotes make up for the majority of the population in this scenario, while homozygotes of mutant and wildtypes oscillate in relative frequency in each generation. When introduced mutants are homozygous and codominant with wildtype loci, Homozygous mutants are the predominant genotype (Figure 6).

Lastly, the question remains which is the minimal release fraction for the population being rescued at an 80% success rate. For this, we calculate rescue probability for every 0.05 introduction fraction value (fraction relative to initial wildtype population of 100), using a monte-carlo estimator and repeating the simulation for each fraction 500 times. The minimal value of 25 individuals suggest we still need a fairly large amount of reintroduced individuals to have a reasonable chance of the population recovering autonomously.

4.1. Limitations and Outlook:

Of course this is only an abstract model trying to grasp the concept of how a metapopulation of lynx behaves in a complex biological ecosystem with multiple layers being linked to each other and building complex relationships. Time is being treated as a discrete variable, while in a real setting, generations are overlapping. The model assumes discrete, non-overlapping generations.

Furthermore, fitness is being linked to two to three distinct genotypes only, and fitness is being linked to a single locus. Also, due to the nature of the equation considering the alle multiplicator and density dependence, populations are not realistically able to approach carrying capacity. Which in turn, comparing to recent population numbers of the Iberian lynx, is also unrealistic when compared to estimated, fundamental carrying capacity of the Iberian Lynx metapopulation (which, depending on literature, are listed as being somewhere between roughly 2'000-10'000). Not to mention various ecological factors occurring in the wild are not taken into account in the model.

This study represents a simplified theoretical framework that abstracts complex ecological realities. The model assumes closed population dynamics without migration, predation or resource limitation beyond logistic density dependence and environmental stochasticity. Due to fitness being assigned to a single locus, the model doesn't allow for polygenic adaptation or epistatic effects that are typical in natural populations.

Furthermore, environmental stochasticity is modeled as independent, normally distributed noise each generation, which does not capture temporal autocorrelation or catastrophic events. Additionally, the model does not incorporate and investigate demographic and rescue dynamics under mutation rates, although mutation rates are implemented and applicable in the defined population functions of this model. Mutation rates would be a crucial and important part of evolutionary rescue, which I ultimately wanted to explore as a vital aspect of rescue. I suggest further extensions and work on this model should investigate the latter aspects for population rescue.

Because of these simplifications, modeled populations do not approach carrying capacity as expected in the real Iberian lynx metapopulation, and rescue thresholds likely underestimate the influence of ecological feedback mechanisms, such as prey dynamics, dispersal corridors, or disease.

Future versions of the model could include age or stage structure, continuous-time processes and eco-evolutionary feedback to reflect more realistic predator-prey and habitat interactions. Despite its simplicity, this model serves as a valuable conceptual tool to illustrate how genetic variation and environmental stochasticity interact to determine the potential for evolutionary rescue in conservation contexts.

References:

literature declarations to be added

Declaration of AI-use: ChatGPT (version 5) was used to assist in the writing structure and brainstorm points of only the Limitations and Abstract. No text or paragraphs were copied or implemented into the report. All of the text was written and created by the author (me).

Author contributions:

to be added