Impact of Frequency of floodings on plant populations

A theoretical model as part of the THEE research practical 2024

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Abstract:

Climate change is having a major impact on a wide range of natural phenomena, including floods. The intensity and frequency of flooding in certain regions has increased and it is projected to increase further. This has huge implications for any community living near a body of water that regularly floods. Some plants are experts at adapting to waterlogging and flood stress, but this advantage may not be present in plant populations that have not previously been exposed to high frequency flooding. This project built a model in R to simulate changes in the composition of a plant population with two genotypes, but only one is well adapted to flood stress. The factor that changed the composition was the frequency of flooding events. The model showed that as the frequency of flooding increases, the maladapted genotype struggles to persist and relies on the well-adapted mutant to provide an evolutionary rescue. In populations exposed to low frequencies, the wild type does not go extinct.

1 Introduction

Changes in the environment can be detrimental for a population. Depending on the state of the environment, and how long this state lasts, a given population can go extinct if it they are not able to adapt (Marrec & Bank, 2023). Climate change for example has a major impact on the frequency and intensity of floods in several regions of the world. Due to increasing rainfall or snowmelt, the anthropogenic influence on such natural events is becoming more relevant (Hirabayashi et al., 2021). Plants are particularly affected by these natural phenomena, as they cannot flee from flooding and must adapt in order to survive. In cases where plants are regularly confronted with large amounts of waterlogging or flooding, they have adapted in different ways. The main problems with large amounts of water are that gas exchange is hindered, and photosynthesis cannot proceed normally due to closed stomata. Toxic metabolites can accumulate and the plant suffers. Plants have different responses to this stress, such as the formation of aerenchyma to improve oxygen transport, antioxidant defence systems, adventitious roots or shifts to different respiration modes (Manghwar et al., 2024).

Within a population, there may be intraspecific differences in how well certain genotypes can cope with these stresses. A study by Reents et al. investigated the influence of the frequency of flooding on different genotypes of a salt marsh grass (Reents et al., 2021). It was shown that within the same species there are genotypes that are better able to cope with high flood frequencies than other genotypes. A similar situation was the subject of this project.

The following system was simulated in this model: A river meadow is regularly flooded, while the frequency of flooding increases due to climate change. The focus lies on a plant population with two genotypes: The wildtype, which is maladapted to floods and waterlogging, and a mutant, which prospers in flooding situations. The parameter of interest is the frequency of floods, respectively the pause in between floods. A sketch of the model can be seen in image 1.

This leads us to the following biological question: What is the impact of the frequency of floodings on the composition and the extinction rates of a plant population?

We hypothesize that the flood-adapted mutant performs an evolutionary rescue, if the frequency of floodings is high and the wildtype goes extinct. At lower frequencies, we expect the wildtype to survive and dominate in the population.
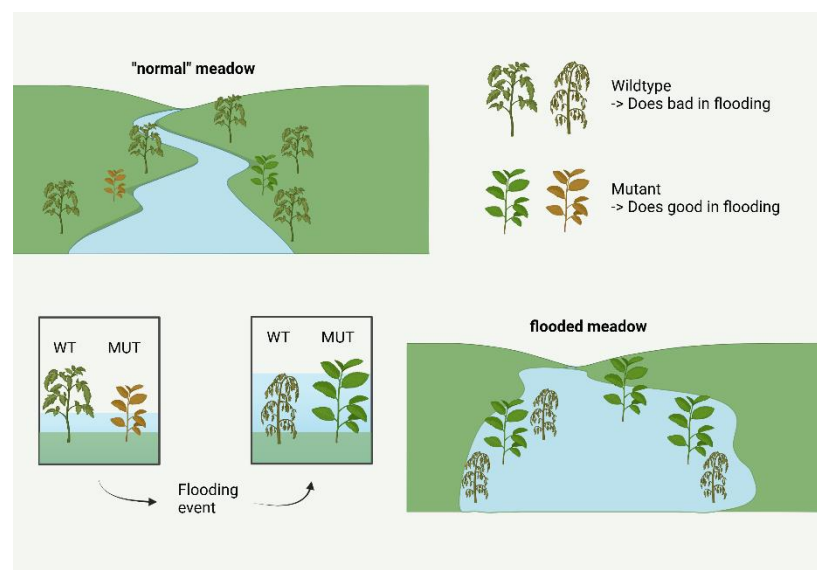

Image 1: Sketch of the model. Two genotypes (wildtype and mutant) react differently to the meadow being flooded. The wildtype does bad, while the mutant thrives during the flooding and vice versa during no-flooding periods.

2 Methods & Model

The R-code for a simple evolutionary rescue model was provided and expanded on. The code was set into a biologically relevant scenario and used to answer the biological question mentioned above.

In addition to the existing code, the first step was to determine the strength of the event. For this, a flooding event was simulated by increasing the decay rate and have the population only be consisting of the wildtype. The mean time it took for the wildtype population to go extinct was taken as a maximum length of an event, everything beyond that would mean, that the population goes extinct after just one event.

After simulating one generation and eventually one population (see chapter 2.1.1), a whole population was simulated under the influence of a fixed frequency of flooding events (see chapter 2.1.2). The flooding was determined by a high decay rate for the wildtype population and high selection coefficient for the mutant. If there was no flooding, the wildtype benefits from a growth rate (negative decay rate) and the mutants are selected against (negative selection coefficient). Before simulating the population, a fixed pause between the flooding (frequency; `t_pause`) and a duration of the flooding (`t_event`) is determined. The time measurement of the model is generation. By partitioning the simulation-run into phases (`ph = 1, 2, 3,` etc.), the model can determine, if it is in a flooding or not. Odd number of phases indicate that the model is in a flood, even number mean the opposite. Depending on whether the current population is in a flooding event or not, the corresponding decay rate and selection coefficients influence the fate of the population. When the phase switches, both variables switch as well.

After successfully simulating an entire population, the next step was to create replicates and simulate different frequencies. For this, the process described above, was looped through different frequencies, using a `for()`-loop. For each pause between the floodings, from 1 to 10 generations, 100 replicates were generated. The model then generated 100 runs for each frequency and saved the data in different data tables. Data on population composition, surviving populations and lengths of the simulations were collected for the analysis.

The last step was to plot and analyse the data that was collected in the simulations, which was all done in R as well.

An overview of all the parameters and variables used can be found on the next page, while the next chapter explains in more detail the process of generating the data.

<u>Parameters</u>

Initial population size of wildtype	1000
Initial population size of mutant	0
Mutation rate	0.001
Duration of flood (t_event)	5 generations
Maximal generation	1000
Number of replicates	100
Stop conditions	Total Population = 0　　　　　OR Total Population = 1.5 * initial WT-Population

<u>Variables</u>

Population size of wildtype and mutation	
Frequency of floodings (t_pause)	1-10 generation pauses (1-20 generation pauses for a few graphs)
Decay rate of WT during floods	0.03
Decay rate of WT during pauses	-0.02
Selection coefficient of mutant during floods	0.05
Selection coefficient of mutant during pauses	-0.015

2.1 Generating the data

This chapter goes into further detail in how the data was generated, which is the basis for the final plots.

After implementing the parameters and variables stated above, the R-code was run. The generated data of each code chunk was used for further plotting.

2.1.1 Simulation one population of population size change

Simulating the first code-chunk, "Simulating one generation of population size change" resulted in 84 wildtype (WT) and 0 mutants (MUT) (Table 1). This code-chunk tracks the population from one generation to another, which is the basis of our code.
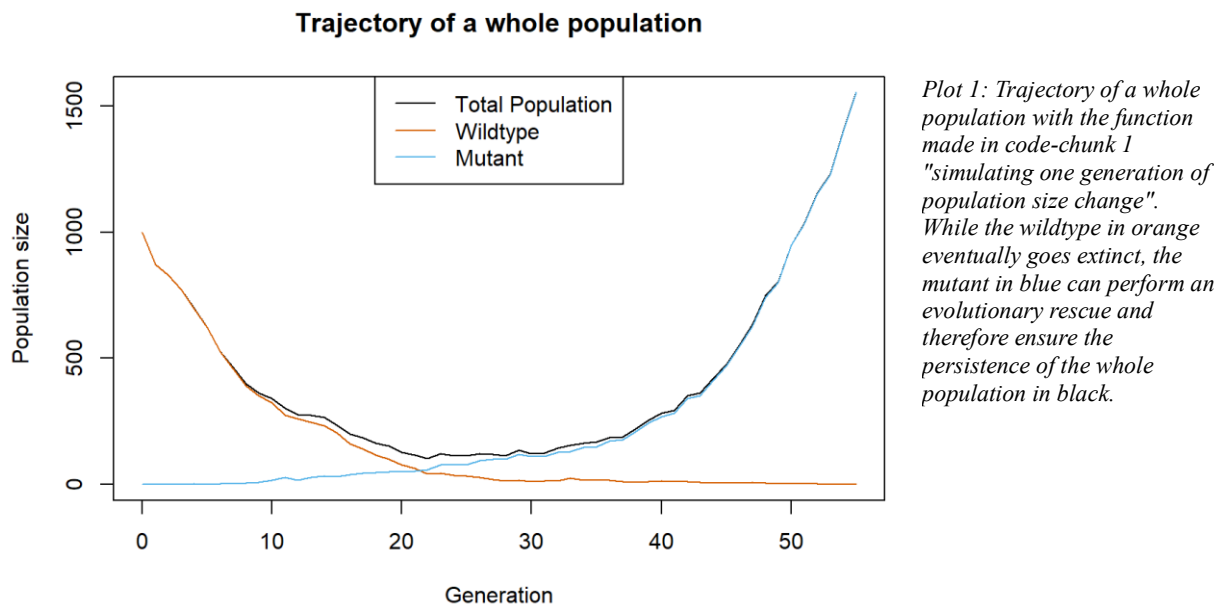
Table 1: Wildtype and mutant population size after simulating one generation with the respective variables and parameters

Wildtype	84
Mutant	0

The second code-chunk "Simulate a population trajectory" simulates a whole population. It tracks the population from the beginning until the population either goes extinct or reaches 1.5 times the initial wildtype population, which can be interpreted as a sign for the well-being of the population. The respective numbers of "a" (WT) and "A" (MUT) are saved in a data table (Table 2) and plotted (Plot 1).

Table 2: Last six generations after simulating a whole population with the corresponding population size of wildtype and mutant. The variables and parameters used here are

Generation	Wildtype	Mutant
50	2	948
51	3	1030
52	3	1151
53	1	1230
54	1	1396
55	0	1554

Trajectory of a whole population

Plot 1: Trajectory of a whole population with the function made in code-chunk 1 "simulating one generation of population size change". While the wildtype in orange eventually goes extinct, the mutant in blue can perform an evolutionary rescue and therefore ensure the persistence of the whole population in black.
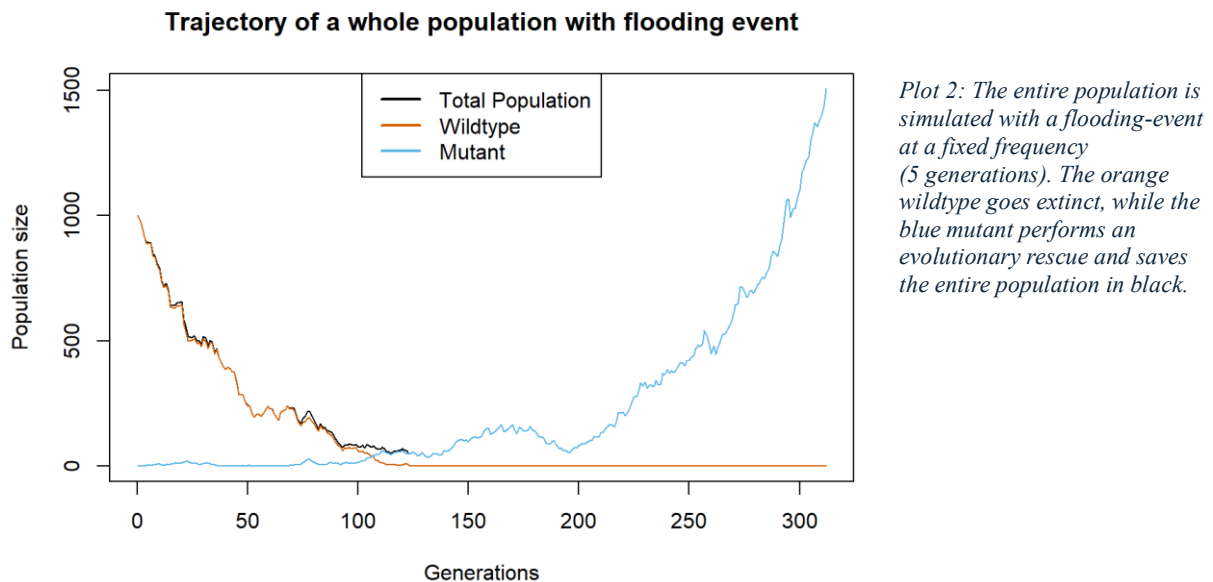
2.1.2 Simulating a whole population with a fixed event

The next step was to introduce the flooding-event, of which the frequency should further on be changed and eventually looked at the effect this has on the entire population. As in 2.1.1 the respective numbers of wildtype and mutant were saved in a data-table and then plotted in plot 2. Table 3 shows the first and last five generations with the corresponding wildtype and mutant population numbers.

Table 3: Simulating one whole population with a fixed event. The whole population was simulated with an event occurring at a fixed frequency and the table shows the first and last five generations with the corresponding wildtype and mutant numbers.

Generations	Wildtype	Mutant
0	1000	0
1	896	1
2	792	4
3	722	2
4	652	5
5	571	4
…	…	…
307	0	1372
308	0	1356
309	0	1382
310	0	1397
311	0	1440
312	0	1507

Trajectory of a whole population with flooding event

Plot 2: The entire population is simulated with a flooding-event at a fixed frequency (5 generations). The orange wildtype goes extinct, while the blue mutant performs an evolutionary rescue and saves the entire population in black.

2.1.3   Generating multiple replicates at different frequencies and extracting the data

After simulating a single population at a given frequency, the next step was to simulate multiple populations at different frequencies. With fixed initial values, the code ran the function from 2.1.2. for each frequency and saved the values in different data-tables. For each frequency, 100 replicates were made and at the end there were four different data-tables as output:

- *data_table_Pop* contains 100 replicates of each frequency with the corresponding final population size and the final generation (generation at which either stop-condition was reached)

- *data_table_Nw* contains 100 replicates of each frequency with the corresponding wildtype population size and the final generation
- *data_table_Nm* contains 100 replicates of each frequency with the corresponding mutant population size and the final generation
- *data_table_comp* contains 100 replicates of each frequency with the corresponding proportion of wildtype and mutant compared to the whole population

Additionally, the surviving ratios of the wildtype and mutant were calculated and incorporated in a respective data-table.

3 Results

3.1 Plotting the data

With the generated data, various plots were made. Shown are the most important plots, further plots are found in the appendix.

3.1.1 Extinction rate

Besides the survival rate, the extinction rate was calculated according to the different frequencies. This was done for the entire population (Plot 7 in appendix) and for both the wildtype and mutant individually (Plot 3).
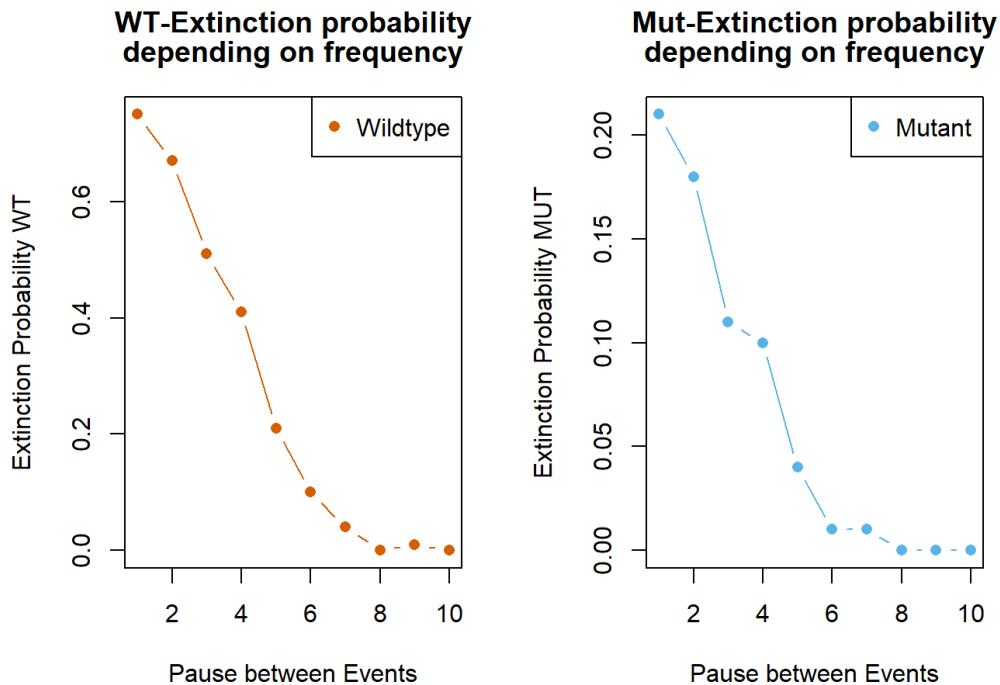

Plot 3: Extinction probability of the wildtype (left) and of the mutant (right). Note the asymmetrical y-axis. The higher the pause between events, the lower the frequency. The lower the pause between events, the higher the frequency.

Plot 3 shows the different extinction rates of wildtype on the left and the mutant on the right. Both have a similar curve shape, which does make sense, since the presence of the mutant is dependent on the presence of the wildtype due to the given mutation rate. If the wildtype is present, then the population contains a certain number of mutants as well due to the given mutation rate.

The wildtype does not depend on the mutant and is therefore more affected by high frequencies of the floods than the mutant. The wildtype has around 80 % of extinction probability at the highest frequency compared to around 22 % of extinction probability for the mutant. At these high frequencies, it depends on how abundant the mutant genotype is at the time point at which the wildtype goes extinct. If the wildtype goes extinct, the mutant can still be present. The mutant still has an extinction rate though, because in some cases it is not abundant enough and goes extinct. The lower the frequencies get, the more the extinction rate for both the wildtype and the mutant decrease.

3.1.2   Mean proportion of wildtype and mutant

Of those populations that survived, the final composition was calculated. The respective final composition is incorporated in a data-table, which was visualized in a boxplot (Plot 4).
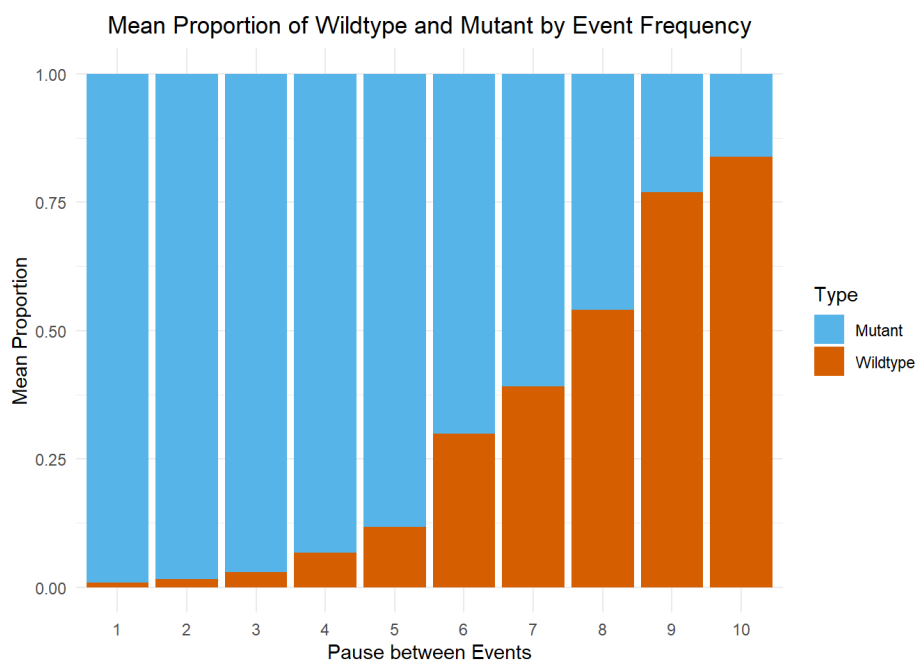
Plot 4: Mean proportion of wildtype and mutant depending on the frequency (1-10). The higher the pause between events, the lower the frequency. The lower the pause between events, the higher the frequency. As can be seen in the plot, at high frequencies the mutant in blue is predominant, while at low frequencies the wildtype in orange is predominant.

For better representation of how the trend looks like, another plot was made with frequencies up to 20 instead of just 10 (Plot 5). Additionally, to get exactly this graph, set.seed(4) → set.seed(12) and set.seed(6) → set.seed(13).
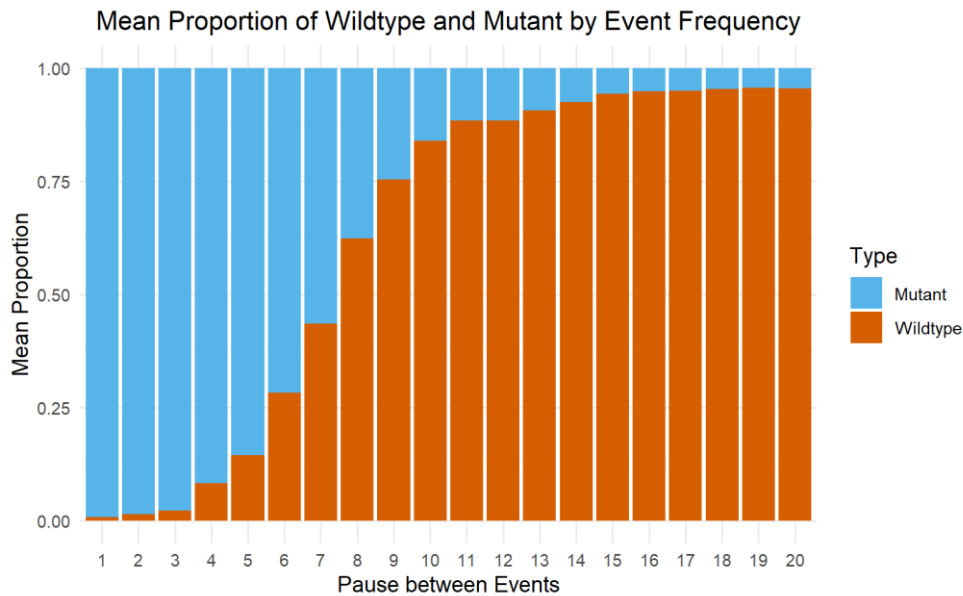
Plot 5: Mean proportion of wildtype and mutant depending on the frequency (1-20). The higher the pause between events, the lower the frequency. The lower the pause between events, the higher the frequency. As can be seen in the plot, at high frequencies the mutant in blue is predominant, while at low frequencies the wildtype in orange is predominant.

Looking at plot 4 and the final population composition of those that survived, a clear trend can be seen. At high frequencies, the mutant makes up the majority of the population while the wildtype is barely present. The lower the frequencies get, the bigger the proportion of the wildtype in the final population gets. When considering that the wildtype does better in low flood-frequencies than the mutant, this is a reasonable result. As shown in plot 5 more clearly, the curve flattens out and the proportion of wildtypes and mutants stays very similar from a certain frequency on. This plateau is explained by the constant mutation rate of wildtypes to mutants, which acts at every generation. Even though the mutants do not persist well during these low frequencies, they still are present at similar proportions due to the mutation rate.

Plot 5 also shows that on average the final population is polymorphic, meaning that both genotypes are present yet at different proportions.

4 Discussion

The aim of this model was to show the effect of different flooding-frequencies on a plant population. As expected, changing the frequency (= the pause between the floodings) leads to different survival and extinction rates of the genotypes as well as different compositions of the population.

It was shown that especially the extinction rate of the wildtype changes drastically with increasing flooding frequencies (Plot 3). The more frequent such an environmental event is, the more likely the wildtype is to go extinct, thus confirming the first hypothesis. This process is also described in other papers, which strengthens our findings (Marrec & Bank, 2023). Although the authors focused their findings on microbial resistance, the results for the periodic

changes in the environment matched our findings. Apart from microbes and drugs, the results could apply to many plants, hence the increasing probability of floodings could strongly decline a given population and even drive it to extinction. Depending on the abundancy of the mutant, the population can be rescued by evolutionary rescue. If the mutant is abundant enough at the time the wildtype goes extinct, it can persist on its own and the species is still present in that specific environment. For a species it is therefore better to already have different genotypes, meaning being a heterogeneous population, than just have one specific genotype.

Depending on the frequency of the events, the proportion of mutant and wildtype in the population can vary (Plot 4 and 5). At higher flooding frequencies, the mutant is more likely to predominate, thus confirming the second hypothesis. The former less adapted genotype takes over and ensures the persistence of the population.

For the entire population it might be better to have an intermediate proportion of wildtype and mutant to be flexible enough to respond to different frequencies of floodings. If the proportion is one-sided, it could take too long for the population to shift the population composition. Keeping this composition intermediate ensures the ability for a quick response.

Having a flood resistant genotype and ensuring the population survives during floods is crucial for biodiversity and other aspects, for example food production: There are studies done, for example on rice to make it flood resistant, either by selective breeding or genomics (Haque et al., 2023).

Apart from maintaining the biodiversity, a study done in 2013 showed that plant species grown in a species-rich environment are also less negatively affected by floodings compared to species that grew in a species-poor environment (Wright et al., 2017). Therefore, maintaining a species can also help other species through flooding-events.

5   Conclusion

After simulating a haploid population with two genotypes and different frequencies it can be concluded that the frequency does affect the population. With high frequency of floods, the wildtype goes extinct, and the mutant can persist if it is numerous enough to perform an evolutionary rescue. At low frequencies, the wildtype persists but the mutant does not go extinct due to the mutation rate. Hence, mutations become more important for the population if floods become more frequent.

Furthermore, containing a flood-resistant mutant in the population to start with also allows for a quick response, since the mutant does not have to evolve in the first place but is already present in the population, which then can be saved more rapidly.

6   Limitations and further steps

This model contains various limitations and assumptions, which can be accounted for in future projects.

The population is haploid, a further step here would be to implement diploidy with heterozygosity. This would make the model more interesting and more applicable to nature.

The model also contains multiple pre-determined parameters and variables which can be made variable in follow-up research. For example, the mutation is now fixed to 0.001. This rather high mutation rate can be decreased and then investigated on the effect of a more realistic mutation rate. Or the mutation rate can change depending on if the system is flooded or not. The switching of mutation rate due to stress has been shown to occur in other studies already (MacLean et al., 2013).

A backmutation can be included in further research. This can solve the issue, that the mutation cannot go extinct by itself and only if the wildtype goes extinct. Having a backmutation, the mutant genotype can go extinct even though the wildtype would still be present.

Concerning the flooding-events, the strength and / or duration of the floods can be adjusted or made flexible. Even stochasticity can be implemented, so that the floods occur at a certain probability and not after fixed intervals like done in this model. This can lead to even faster extinction rates, as was shown by Marrec and Bank (Marrec & Bank, 2023).

The biggest limitation probably was time. This project was part of a three-week course in Theoretical Ecology and Evolution, so the model had to be accomplished in given time.

This project and model should serve as a strain of thought and can be expanded on in a variety of other different directions than mentioned above.

7   Acknowledgements

8   Authors contributions

The base code was provided by Prof. Dr. Claudia Bank, which we expanded with the help Dr. Catalina Chaparro, Dr. Loïc Marrec and ChatGPT, so that it fulfils our requirements and is able to answer our biological question.

9 References

Haque, M. A., Rafii, M. Y., Yusoff, M. M., Ali, N. S., Yusuff, O., Arolu, F., & Anisuzzaman, M. (2023). Flooding tolerance in Rice: adaptive mechanism and marker-assisted selection breeding approaches. In *Molecular Biology Reports* (Vol. 50, Issue 3, pp. 2795–2812). Springer Science and Business Media B.V. https://doi.org/10.1007/s11033-022-07853-9

Hirabayashi, Y., Alifu, H., Yamazaki, D., Imada, Y., Shiogama, H., & Kimura, Y. (2021). Anthropogenic climate change has changed frequency of past flood during 2010-2013. *Progress in Earth and Planetary Science*, *8*(1). https://doi.org/10.1186/s40645-021-00431-w

MacLean, R. C., Torres-Barceló, C., & Moxon, R. (2013). Evaluating evolutionary models of stress-induced mutagenesis in bacteria. In *Nature Reviews Genetics* (Vol. 14, Issue 3, pp. 221–227). https://doi.org/10.1038/nrg3415

Manghwar, H., Hussain, A., Alam, I., Khoso, M. A., Ali, Q., & Liu, F. (2024). Waterlogging stress in plants: Unraveling the mechanisms and impacts on growth, development, and productivity. In *Environmental and Experimental Botany* (Vol. 224). Elsevier B.V. https://doi.org/10.1016/j.envexpbot.2024.105824

Marrec, L., & Bank, C. (2023). Evolutionary rescue in a fluctuating environment: Periodic versus quasi-periodic environmental changes. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1999). https://doi.org/10.1098/rspb.2023.0770

Reents, S., Mueller, P., Tang, H., Jensen, K., & Nolte, S. (2021). Plant genotype determines biomass response to flooding frequency in tidal wetlands. *Biogeosciences*, *18*(2), 403–411. https://doi.org/10.5194/bg-18-403-2021

Wright, A. J., de Kroon, H., Visser, E. J. W., Buchmann, T., Ebeling, A., Eisenhauer, N., Fischer, C., Hildebrandt, A., Ravenek, J., Roscher, C., Weigelt, A., Weisser, W., Voesenek, L. A. C. J., & Mommer, L. (2017). Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytologist*, *213*(2), 645–656. https://doi.org/10.1111/nph.14185

10 Appendix

10.1 Extinction and survival rate

### 10.1.1 Survival-ratio of the wildtype

With the data gained in 2.1.3, the survival-ratio of the wildtype was plotted. The x-axis indicates the pauses between events, while the y-axis indicates the survival rate. The higher a pause, the lesser is the event-frequency. Therefore, the lower the pause between the events, the higher is the flooding-frequency. The plot just shows the curve for the wildtype.

Survival Ratio of wildtype depending on the frequency of events
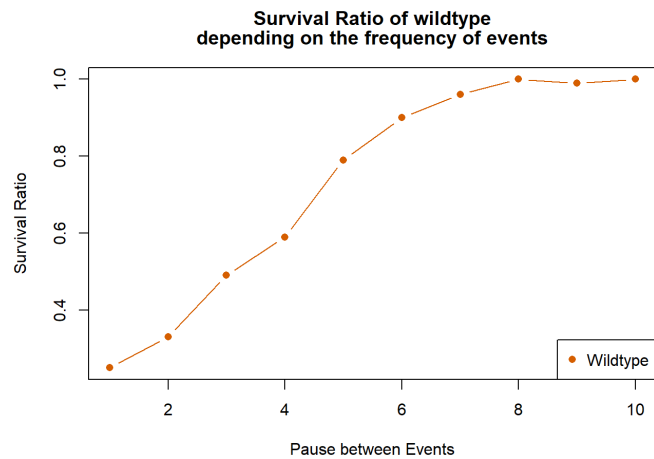
Plot 6: Survival rate of the wildtype according to different frequencies. The lower the pause between events, the higher the frequency. The higher the pause between events, the lower the frequencies. As can be seen in the graph, the lower the frequencies get (high x-value) the survival rate of the wildtype tends towards 1.

### 10.1.2 Extinction rate of the whole population

Plot 7 shows the extinction probability for the whole population at different frequencies. The lower the frequencies get, the lower the extinction rate for the population. This complements plot 3 with the individual extinction rates for wildtype and mutant, since the overall shape is similar.

Extinction rate depending on frequency
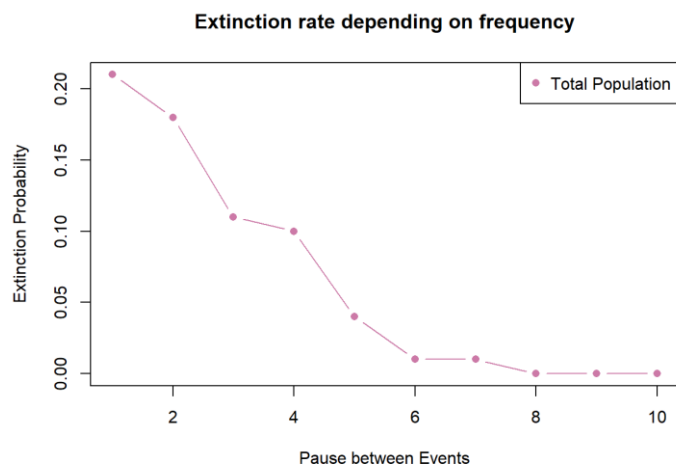
Plot 7: Extinction probability of the entire population according to the frequency. The higher the pause between events, the lower the frequency. The lower the pause between events, the higher the frequency. As the events get less frequent (high x-value) the total population tends to survive every time.

10.2 Extinction-generation

The final generation can also be reduced to the extinction generation depending on the frequency. For this, the generation, at which the entire population went extinct, was counted and plotted against the frequency.
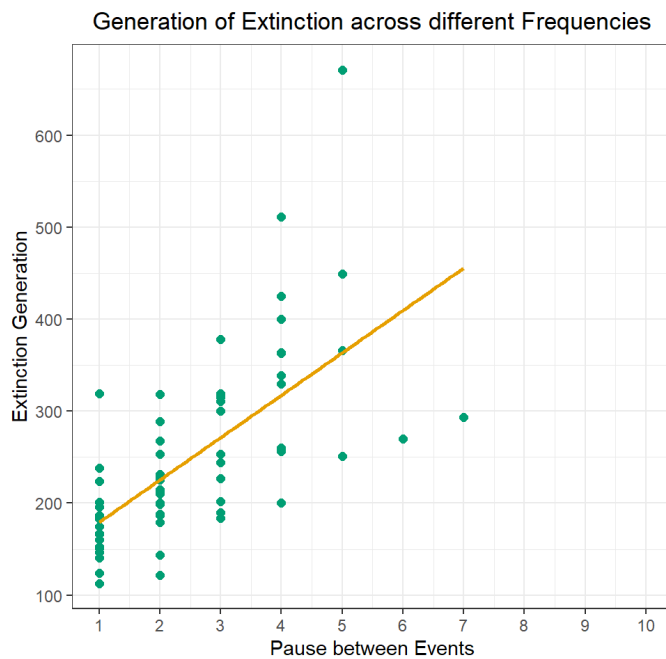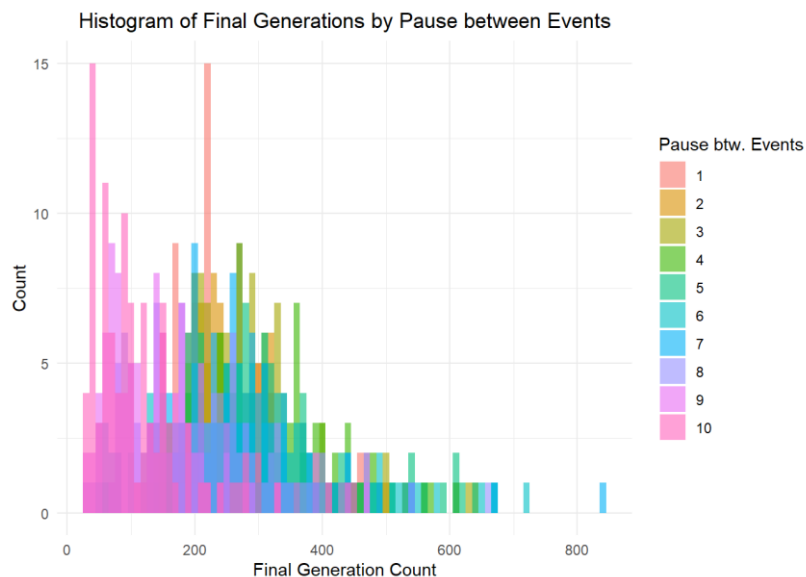

Plot 8: Generation of extinction depending on the frequency. The higher the pause between the events, the lower the frequency. The lower the pause between the events, the higher the frequency. The population goes extinct at a slower rate with increasing pauses between the events. From a certain pause-duration onwards, no extinction are found.

10.3 Distribution of the final generation

Another interesting aspect to look at is the distribution of the final generation depending on the frequency. For every frequency, the mean of the final generation was taken and incorporated in a data-table. With this data-table a boxplot (Plot 9) as well as a histogram (Plot 10) was made to visualize this relationship.
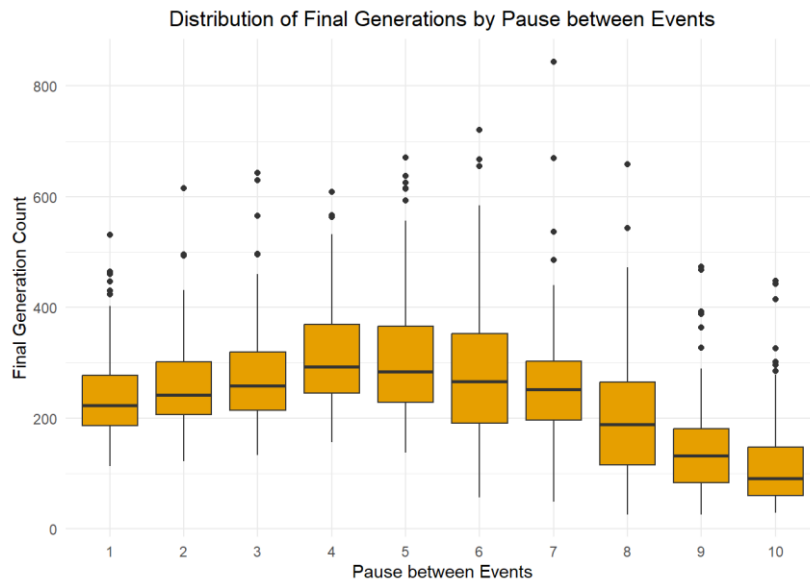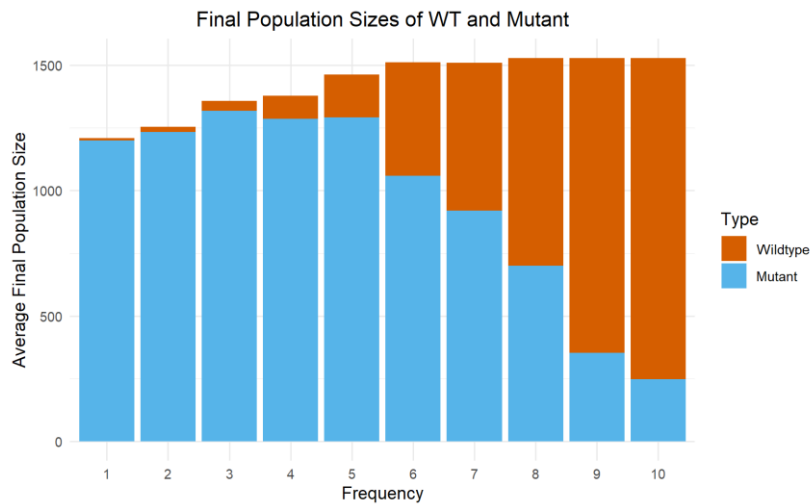

Plot 9: Boxplot of the final generation number depending on the frequency. The higher the pause between the events, the lower the frequency. The lower the pause between the events, the higher the frequency. Intermediate frequencies showed the larges final generation, meaning they fluctuated the most between the two stop conditions.
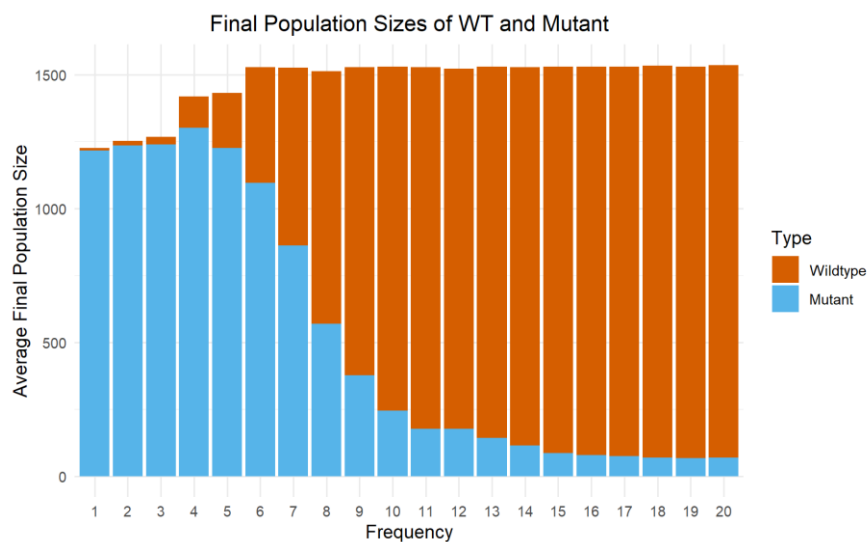

Plot 10: Histogram of the final generation number depending on the frequency. The higher the pause between the events, the lower the frequency. The lower the pause between the events, the higher the frequency. This plot complements the findings in plot 9. The highest "final generation" was found at intermediate pauses between events.

10.4 Final population sizes

In chapter 3.1.2, the barplots show the percentual composition of wildtype and mutant in the final generation. Another way of visualizing the final generation is to look at the effective population sizes. Plots 11 and 12 show the fluctuating population sizes and represent the different proportions of wildtype and mutant at different frequencies.

Plot 11: Effective population numbers of wildtype and mutant depending on the frequency (1-10). The higher the pause between events, the lower the frequency. The lower the pause between events, the higher the frequency. As can be seen in the plot, at low frequencies the mutant in blue is predominant, while at low frequencies the wildtype in orange is predominant.

Plot 12: Effective population numbers of wildtype and mutant depending on the frequency (1-20). The higher the pause between events, the lower the frequency. The lower the pause between events, the higher the frequency. As can be seen in the plot, at low frequencies the mutant in blue is predominant, while at low frequencies the wildtype in orange is predominant.