

# 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 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 haven't previously been exposed to high frequency flooding. This project built a model in R to simulate changes in the composition of a plant population where two genotypes are present, 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 has no problem surviving.

# 1 Introduction

Climate change 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). Among various animal species, 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.

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 suggest, that the wildtype survives and dominates in the population.

# 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 then taken as a maximum length of an event, everything beyond that would mean, that the population goes extinct after just one event.

Then a whole population was simulated under the influence of a fixed frequency of flooding events. The mutant was added to the model and the flooding was determined by a high decay

rate for the 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;  $t_{\text{pause}}$ ) and a duration of the flooding ( $t_{\text{event}}$ ) is determined. The time measurement of the model is generation. By partitioning the simulation run into phases ( $ph = 1, 2, 3, \text{etc.}$ ), 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 a whole 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.

### Parameters

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

### Variables

Population size of wildtype and mutation	
Frequency of floodings ( $t_{\text{pause}}$ )	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

### 3 Results

After implementing the various parameters and variables, the code was ready to be run and generate data with which then various plots could be made. The whole R-code is run with the variables and parameters stated in chapter 2 “Methods and Model”. The generated data of each code chunk can be used for further plotting. For further information, on what each code-chunk exactly does, see chapter 2 “Methods and Model”.

#### 3.1 Generating the data

##### 3.1.1 Simulation one population of population size change

The results of simulating the first code-chunk, “Simulating one generation of population size change”, are 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.

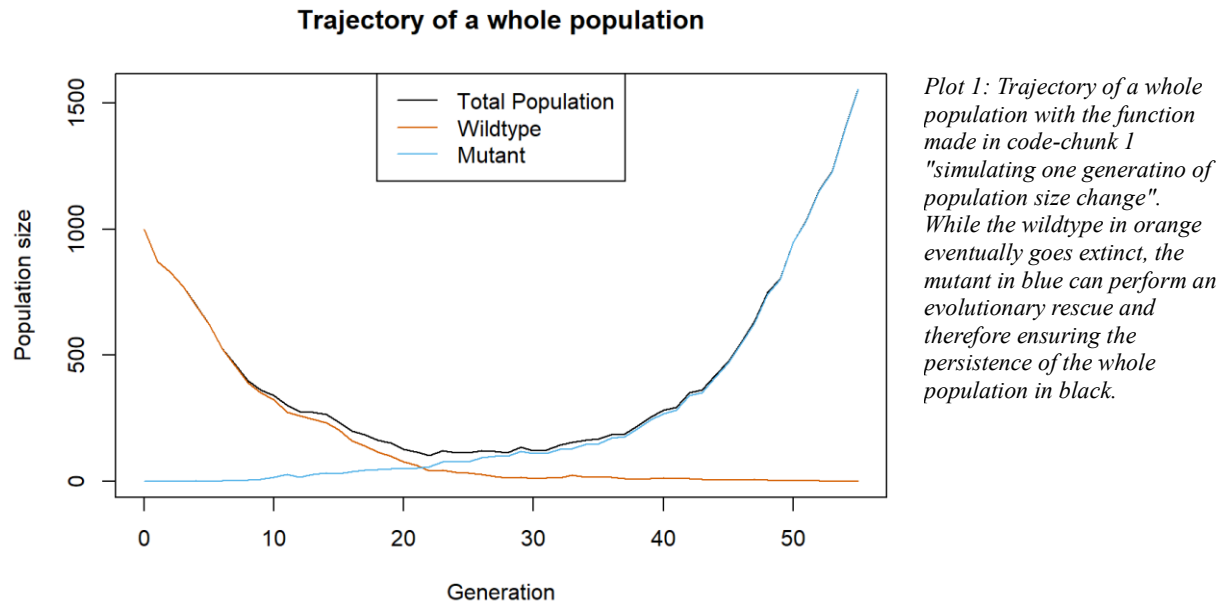
*Table 1: Wildtype and mutant population size after simulating one generation with the respective variables and parameters*

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. The respective numbers of “a” (WT) and “A” (MUT) are saved in a data table (Table 2) and the results are 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

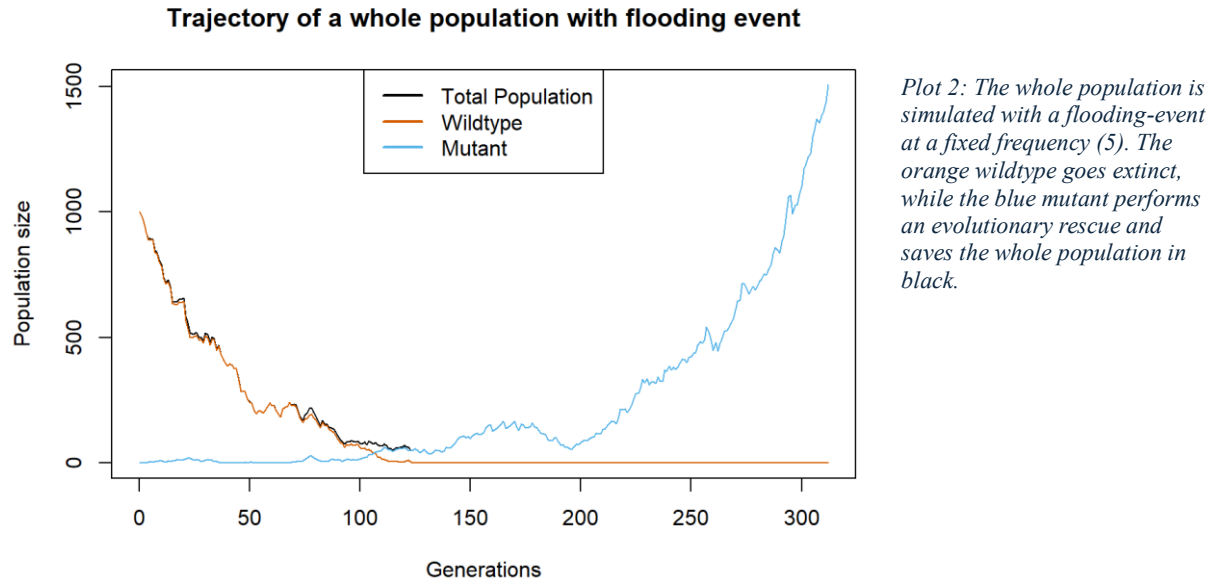


### 3.1.2 Simulating a whole population with a fixed event

The next step is to introduce the flooding-event, of which the frequency should further on be changed and eventually look at the effect this has on the whole population. As in 3.1.1 the respective numbers of wildtype and mutant are saved in a data-table and these then plotted in plot 2. Table 3 below 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



### 3.1.3 Generating multiple replicates at different frequencies and extracting the data

After simulating a single population at a given frequency, the next step is to simulate multiple populations at different frequencies. With fixed initial values, for each frequency the code runs the function from 3.1.2. and saves the values in different data-tables. For each frequency 100 replicates are made and at the end there are 4 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

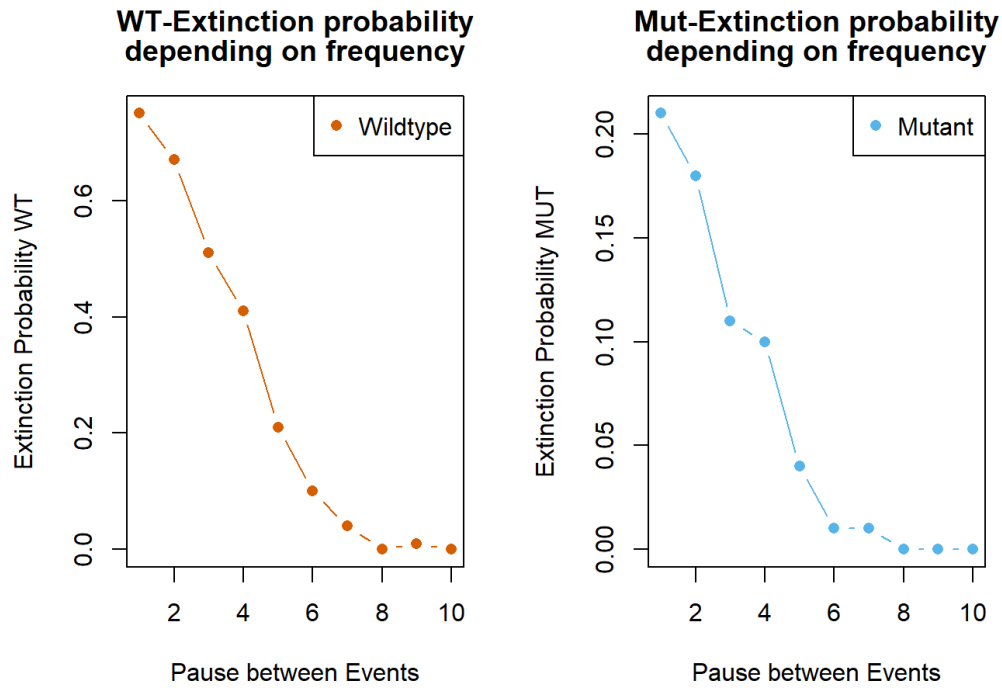
Additionally, the surviving ratios of the wildtype and mutant were calculated and incorporated in a respective data-table.

## 3.2 Plotting the data

In this chapter the main graphs are shown. Further graphs are found in the appendix.

### 3.2.1 Extinction rate

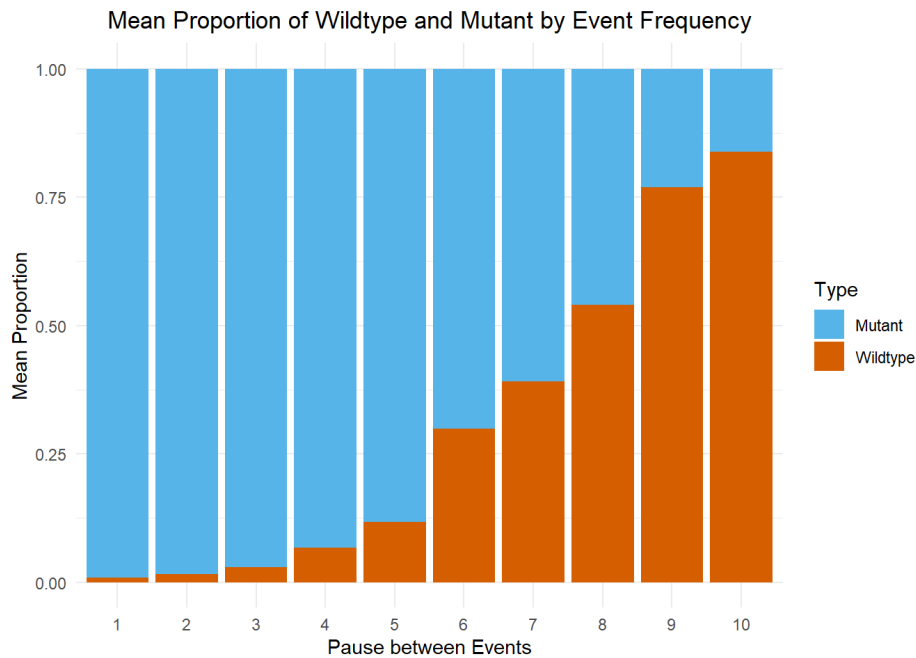
Besides the survival rate the extinction rate can also be calculated according to the different frequencies. This can be done for the whole population (Plot 7 in appendix) and for both the wildtype and mutant individually (Plot 3).



*Plot 3: 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 low frequencies the mutant in blue is predominant, while at low frequencies the wildtype in orange is predominant.*

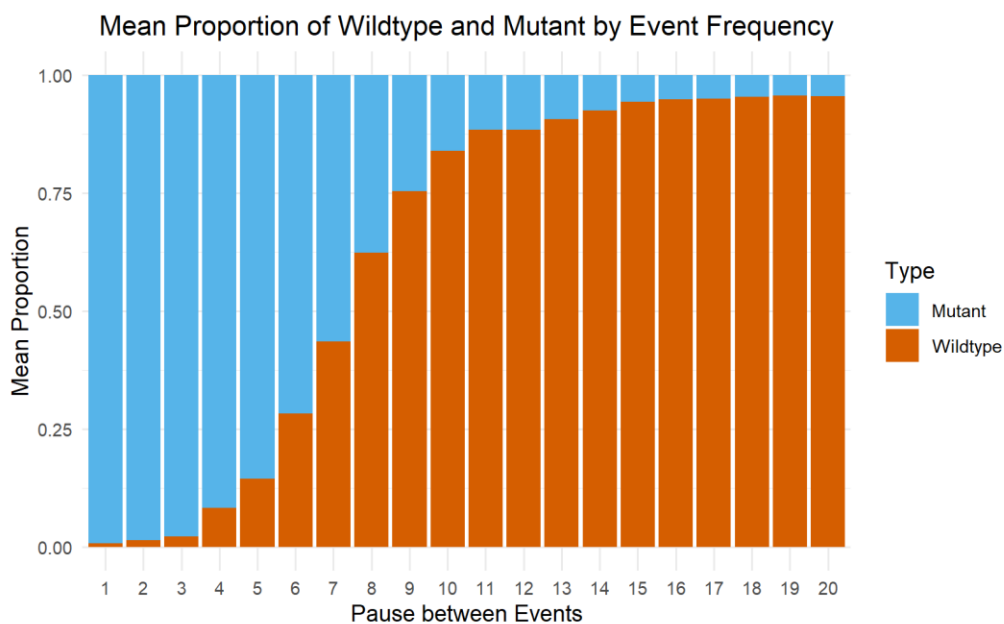
### 3.2.2 Mean proportion of wildtype and mutant

Of those populations that survived, the final composition can be calculated. The respective final composition is incorporated in a data-table, which can be visualized in a boxplot (Plot 4).



Plot 4: 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 low 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: 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.



## 4 Discussion

The aim of this model was to show the effect of different flooding-frequencies on a plant population. 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.

### 4.1 Extinction rate

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. The wildtype does not depend on the mutant and is therefore more affected by high frequencies of floods than the mutant is. 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 mutant is abundant enough when the wildtype goes extinct, evolutionary rescue can be performed. In this cases, the mutant can persist on its own and is not dependent anymore on the mutation rate from wildtype to mutant. This explains the lower extinction frequency of the mutant compared to the wildtype at these high frequencies. If the wildtype goes extinct, the mutant does not necessarily go extinct as well. The mutant still has an extinction rate, because in some cases it is not abundant enough and also goes extinct. The lower the frequencies get, the extinction rate for both the wildtype and the mutant decrease. The wildtype does better at these low frequencies and due to the mutation rate, there will always be some mutants present in the population. These results in plot 3 confirm our first hypothesis, which states that at lower frequencies the wildtype persists better than at high frequencies. The higher the frequencies are, the more likely the wildtype population goes extinct.

### 4.2 Population composition

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 wildtypes 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, from a certain frequency on, the curve flattens out and the proportion of wildtypes and mutants stays very similar. This plateau is explained by the 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. This graph confirms our second hypothesis, which states that the higher the frequencies of floods get, the more likely the mutant takes over. Since this graph only shows the populations that survived, it can be concluded that at low frequencies the mutants performed an evolutionary rescue. The wildtype is likely to go extinct (see plot 3) and if the population survives it is mostly made up of mutants. Plot 5 also shows that on average the final population is polymorphic, meaning that both genotypes are present yet at different proportions.

For the whole 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 many studies done 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 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. Therefore, 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 then the mutant does not have to evolve in the first place but is already present in the population which then can be saved.

## **6 Limitations and further steps**

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

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

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

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

Concerning the flooding-events, the strength and / or duration of the floods can be adjusted or made flexible. Even stochasticity could be implemented, so that the floods occur at a certain probability and not after fixed intervals like in this model.

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

## 7 Acknowledgements

We would like to thank the whole THEE research practical team and especially Prof. Dr. Claudia Bank, Dr. Catalina Chaparro and Dr. Loïc Marrec for their help developing this model in this rather short time.

## 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

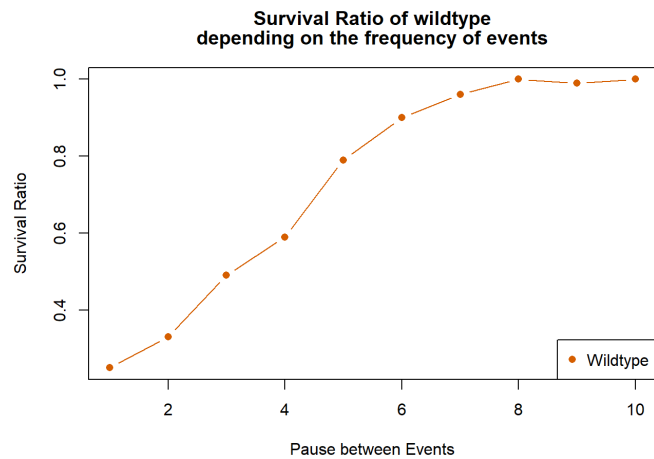
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## 10 Appendix

### 10.1 Extinction and survival rate

#### 10.1.1 Survival-ratio of the wildtype

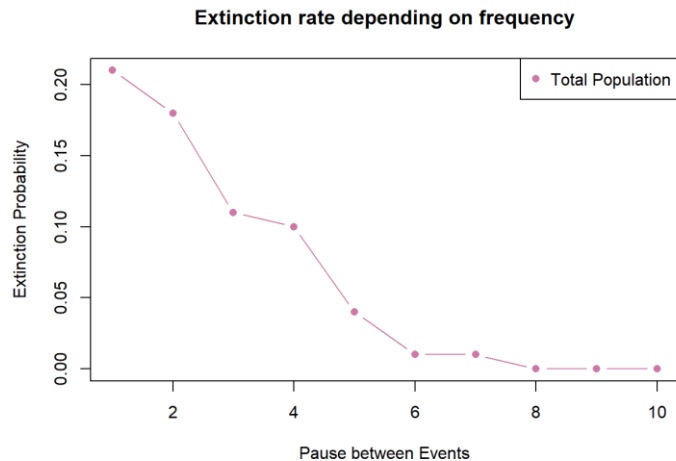
With the data gained in 3.1.3, the survival-ratio of the wildtype was plotted. On the x-axis the pauses between events are indicated. The higher a pause, the lesser is the event-frequency. Therefore, the lower the pause between the events, the higher is the flooding-frequency. On the y-axis is the survival rate indicated. The plot just shows the curve for the wildtype.



*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

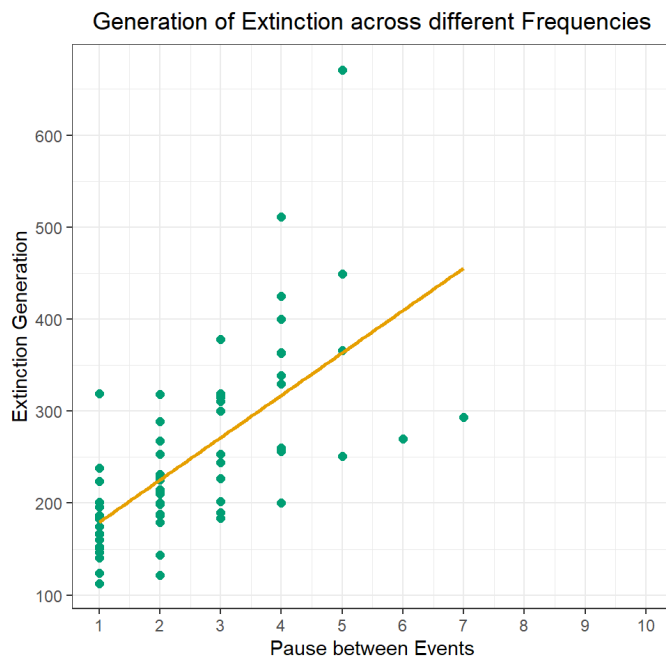
Plot 7 shows the extinction probability for the whole population at different frequencies. The lower the frequencies get, the lower the extinction rate for the population. This complements plot xy with the individual extinction rates for wildtype and mutant, since the overall shape is similar.



*Plot 7: Extinction probability of the whole 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.*

## 10.2 Extinction-generation

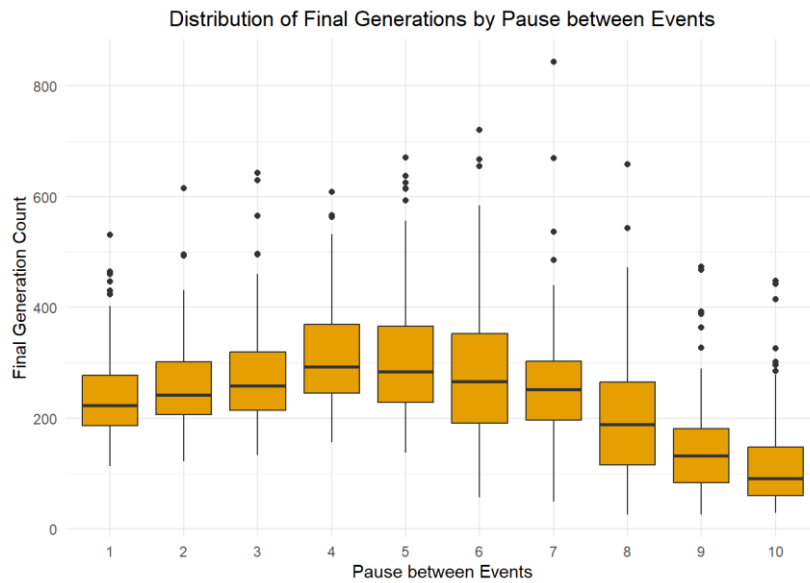
The final generation can also be reduced to the extinction generation depending on the frequency. For this, the generation at which the whole population went extinct was counted and plotted against the frequency (Plot 8).



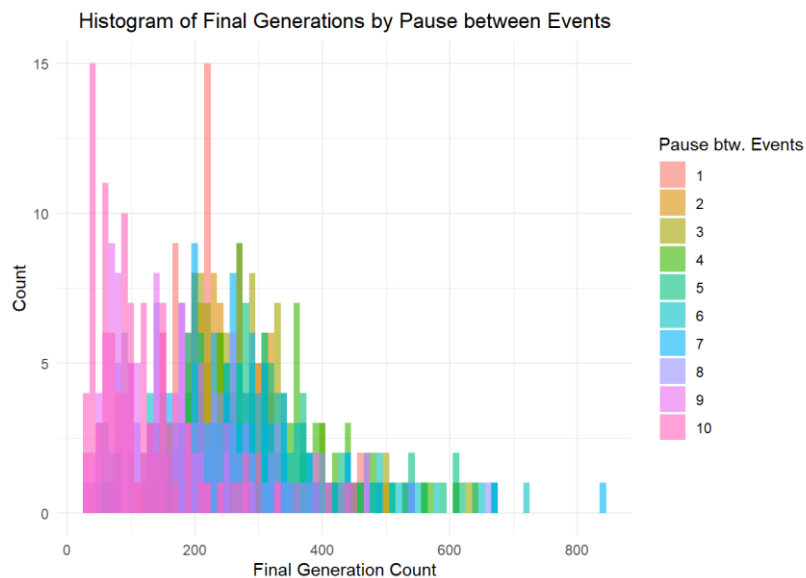
*Plot 8: Generation of extinction depending on the frequency. The higher the pause between the events, the lower the frequency. The lower the pause between the events, the higher the frequency.*

### 10.3 Distribution of the final generation

Another interesting aspect is to look at 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) is made to visualize this relationship.



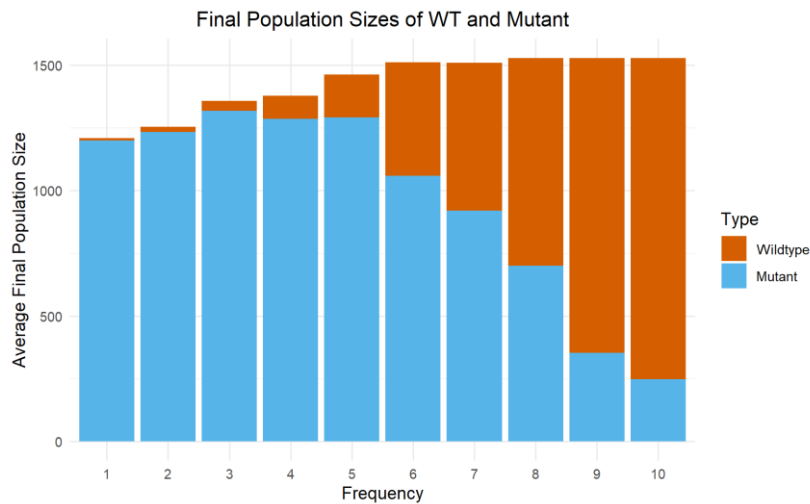
Plot 9: Boxplot of the final generation number depending on the frequency. The higher the pause between the events, the lower the frequency. The lower the pause between the events, the higher the frequency.



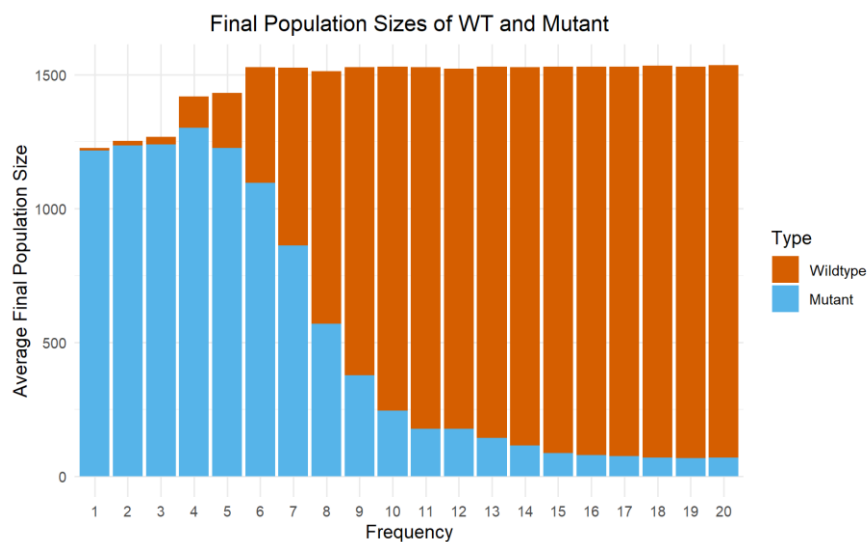
Plot 10: Histogram of the final generation number depending on the frequency. The higher the pause between the events, the lower the frequency. The lower the pause between the events, the higher the frequency.

## 10.4 Final population sizes

In chapter 3.2.2 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 xy-xy also 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.*