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"A Model for the Maintenance of Polymorphisms under Temporally Fluctuating Selection"

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1 Acknowledgements

Ich möchte an dieser Stelle bei meinem Betreuer, Joachim Hermisson, für seine Übersicht, guten Willen, einsichtsvollen Kommentaren und den aufregenden Themenvorschlag aufs Herzlichste bedanken. Auch Meike Wittmann, die mich mit klugen Anregungen, großer Hilfsbereitschaft und produktiven Diskussionen, stets unterstützt hat, bin ich zu großem Dank verpflichted. Zuletzt will ich meine Familie, die mir immer schon ein Fels war, hier mit tiefer Verbundenheit erwähnen.

2 Introduction

The causes for the maintenance of polymorphisms in populations are a long standing question in population genetics. In haploids competition between alleles mirrors competition between species, where the competitive exclusion principle asserts that among competing species only one should persist, when they compete for a single common resource. In diploids polymorphisms can be additionally maintained with the help of overdominance. In this case heterozygotes have higher fitness than either homozygote, leading to rare alleles always having an advantage. However, overdominance is not always given.

Some explanations for the maintenance of polymorphism use spatial variation and the literature is rife with models how spatial heterogeneity can preserve polymorphsims.

Environments not only fluctuate spatially, but also temporally. All organisms are subject to changing environmental conditions. These conditions may impose changes in selection pressures. However first investigations on whether temporal fluctuation can preserve heterogeneity proved not as promising in haploids [Dem55, HJ63, Gil73, Kim54]. Originally population genetics showed that clonal polymorphisms cannot be preserved by temporal fluctuations in environment. To see this consider competition between two alleles in an infinite population of asexual clones. Either one of these increases in frequency across a series of environments, if the product of its relative fitnesses is greater than one. Analogously the other one increases in frequency if the same product is smaller than one, leading to coexistence only if the product of selection parameters is exactly one, which can be considered very unlikely [HJ63]. Even then only one would persist for long in a stochastic context, due to both alleles being selectively neutral.

After these original results where published, other mechanisms have been identified that could preserve polymorphisms in temporally fluctuating environments. The storage effect works with overlapping generations and a life cycle with selected and unselected phases

and can maintain polymorphisms[CW81]. Additionally relative nonlinearity can preserve polymorphisms [Che00].

More recent work by Yi and Dean has produced models that yield coexistence, by doing away with the implicit assumption of unbounded growth and validated this model with experimental evidence.[YD13, Dea05]. For their experimental work they considered two clonal *Esterichia coli* populations competing in two consecutive environments. Those were changed whenever the clones had reached a fixed concentration. Once they did they were inserted at a fixed lower concentration in the next environment [YD13]. This could lead to coexistence. Once one type of *E. coli* was rare the time in an environment where it was at a selective disadvantage was short, since the common population reached the density for transfer quickly, while the time where it was at an advantage was longer, due to the common type taking more time to reach the target density.

While this provided a simple model in which clonal heterogeneity could be preserved, it is not realistic in ecological circumstances. In particular, there is no one conducting an experiment in nature, reducing and transferring populations once they reach a fixed density. There is a gap in the literature regarding ecologically relevant models. This gap is relevant since genetic diversity in several species is claimed to be preserved by temporal fluctuation.

There is evidence of such mechanisms being in place in passerines. It was found that heritable variation in behaviour gave advantages dependent on the population density. Faster explorers were favoured under lower densities, but slower explorers under higher densities [NTU$^+$16].

Drosophila species have long been considered important in genetic research [BDS$^+$10, OtKN$^+$, TSF$^+$11]. In particular recent findings [BBO$^+$14] suggest seasonal variation as preserving factor of genetic polymorphisms in Drosophila. Polymorphisms implicated with starvation tolerance changed in frequency throughout the season, likely giving an advantage at high densities..

To model this purported mechanism, this thesis treats a series of stochastic and deterministic models with two seasons, one constituting population growth, the other one population decline in order to model preservation of polymorphisms in Drosophila and to show that diploid overdominance is not necessary to achieve survival. Both analytic criteria for survival are derived, as well as simulations of gene frequencies are conducted. The goal is

to transfer the key mechanism identified by Yi and Dean [YD13] to a more ecologically relevant setting and to simplify it further.

3 Results

3.1 Deterministic models and criteria for mutual invasion

3.1.1 Model with exponential growth phase

Two alleles compete at a single locus. There are two environments, called summer and winter. In summer there is an initial growth phase. Here both alleles compete through hard selection, until a certain density is reached. During the hard selection phase, the allele called summer allele carries the advantage and is able to reproduce more quickly than its competitor. Once capacity is reached, the initially disadvantaged winter allele is more competitive and enables greater resource acquisition. This is modelled by a relative selective advantage for the winter allele until the end of the winter. At the end of winter, capacity is set to winter capacity.

Allele A and B have densities x_t and y_t. They start at a combined density K_w, which is the winter capacity, individual densities x_0 and y_0, and increase exponentially until their combined density is K_s with Malthusian rates r_A and r_B. This means their densities are given by

$$\begin{aligned} x_t &= e^{r_A t} x_0 \\ y_t &= e^{r_B t} y_0. \end{aligned} \tag{3.1}$$

Then their relative frequencies are modified according to Wright Fisher with B having advantage $s(t)$, while their total density falls to K_w at time n, where n is the number of generations per year.

In the materials and methods section we arrive at the invasion criterion for an invading winter allele B, where $t_K = \lceil \frac{1}{r_A} \log(\frac{K_s}{K_w}) \rceil \approx \frac{1}{r_A} \log(\frac{K_s}{K_w})$ is the time until capacity is reached in the absence of B, and $t'_K = \lceil \frac{1}{r_B} \log(\frac{K_s}{K_w}) \rceil \approx \frac{1}{r_B} \log(\frac{K_s}{K_w})$ is the time until capacity is reached in the absence of A.

$$1 < \frac{e^{r_B t_K}}{e^{r_A t_K}} * \prod_{t=t_K+1}^{n} (1 + s(t)) \approx (\frac{K_s}{K_w})^{\frac{r_B}{r_A}-1} * \prod_{t=t_K+1}^{n} (1 + s(t)). \tag{3.2}$$

The analogous criterion for the invasion of the summer allele A is

$$1 < \frac{e^{r_A t'_K}}{e^{r_B t'_K}} * \prod_{t=t'_K+1}^{n} (1 + s(t))^{-1} \approx (\frac{K_s}{K_w})^{\frac{r_A}{r_B}-1} * \prod_{t=t'_K+1}^{n} (1 + s(t))^{-1}. \tag{3.3}$$

These are non-contradictory in general, as an example consider $\log \frac{K_s}{K_w} = 2$, $r_A = 2$, $r_B = 1$, $n = 3$ and $s(t) = 1 = const$. Then $t_K = 1$ and $t'_K = 2$. Plugging these values into both inequalities provides true expressions.
Constellations conducive to survival are of further interest and will be derived here. We will denote $r = r_B$ and define $\sigma_A = r_A - r$. The selective advantage of the summer allele during the growth phase then is $s_A := e^{\sigma_A} - 1$. To have some analytic simplification we will assume the advantage of the winter allele to be constant as well, and we denote it with s_B and analogously with the summer allele we define $\sigma_B := \log(1 + s_B)$.

One can derive from (3.2):

$$1 < \frac{e^{r_B t_K}}{e^{r_A t_K}} * \prod_{t=t_K+1}^{n} (1 + s(t)) = e^{-\sigma_A t_K} (1 + s_B)^{n - t_K}. \tag{3.4}$$

Taking the logarithm and rearranging gives us $\frac{\sigma_B}{\sigma_A} > \frac{1}{\frac{n}{t_k}-1}$, and analogous reasoning leads us to the criterion for mutual invasion in this form as:

$$\frac{1}{\frac{n}{t'_k} - 1} > \frac{\sigma_B}{\sigma_A} > \frac{1}{\frac{n}{t_k} - 1}. \tag{3.5}$$

Note here that approximately $\sigma_A = s_A$ and $\sigma_B = s_B$, hence if we want to find a parameter regime where the range of possible selection parameters is largest, while still allowing coexistence, we need to maximize the permissible range for this ratio.

If we take n and t'_K to be fixed, the range $\frac{\sigma_B}{\sigma_A}$ is maximized by minimizing $t_K = \lceil \frac{1}{r+\sigma_A} \log(K_s/K_w) \rceil$. This is an unsurprising circumstance, since the proposed mechanism behind the survival depends on differences between times to reach capacity.

Without loss of generality we can assume $t'_K = \frac{1}{r} \log(K_s/K_w)$ and hence $\log(K_s/K_w) = r * t_K$ leading to

$$t_K = \lceil \frac{r * t_K}{r + \sigma_A} \rceil, \tag{3.6}$$

which is a monotonically increasing function in r that tends to 1 as r goes to 0. This in turn implies $\log(K_s/K_w)$ going to 0 when we keep time to capacity of the winter allele a constant, which almost paradoxically implies that mild winters i.e. scenarios where the summer capacity is only slightly larger and is reached slowly are more conducive to survival than scenarios where it is much larger than the winter capacity and the winter allele has a very high growth rate.

3.1.2 Model with growth phase according to the Ricker model

While the above exponential model yields usable criteria, there is a major discontinuity at the moment summer capacity is reached. The Ricker model has originally been used to model fisheries[Ric54], but has since then been shown to result from within year resource competitions [GK04]. It is defined by the following recursive relationship:

$$x_n = x_{n-1} * \exp(r * (1 - \frac{x_{n-1}}{K})). \tag{3.7}$$

Here x_n is the population size at time n, r is the Malthusian growth parameter and K is the capacity. This recursion can be extended to two competing populations x_n and y_n.

$$\begin{aligned} x_n &= x_{n-1} * \exp(r_x * (1 - \frac{x_{n-1} + y_{n-1}}{K})) \\ y_n &= y_{n-1} * \exp(r_y * (1 - \frac{x_{n-1} + y_{n-1}}{K})). \end{aligned} \tag{3.8}$$

Here the populations have a common capacity K, but different growth parameters r_x and r_y. Note that as long as densities are low, the populations behave exponentially, but when they approach capacity, growth comes to a halt. This property enables a continuous transition from exponential to constant behaviour that was missing in the exponential model.

To apply this to seasonally fluctuating selection, consider alleles A and B. Their frequencies x_t and y_t increase according to a Ricker model with capacity K_s and growth rates r_A and r_B for t_s generations. Then their relative frequencies change under relative selection for t_w generations, where allele B has an advantage of s. Then their total sum of densities is set to K_w.

If summer is modelled by the Ricker model the time until we reach high density depends on which allele is common. To further illustrate this consider figure 3.1, which shows a simulated invasion by the summer type and the winter type respectively. When the summer type is common, the phase of no growth is reached faster, giving the summer allele a relative disadvantage.

In the material and methods section invasion criteria for rare B and rare A are derived, which are respectively

$$1 < (1+s)^{t_w} * \left(\frac{x_{t_s}}{K_w}\right)^{(\frac{r_B}{r_A} - 1)}. \tag{3.9}$$

$$1 < (1+s)^{-t_w} * \left(\frac{y_{t_s}}{K_w}\right)^{(\frac{r_A}{r_B} - 1)}. \tag{3.10}$$

Simulations confirm this prediction and find surviving polymorphisms. Figure 3.2 gives the first 500 generations of a stable polymorphism, where $r_A = 0.9$, $r_B = 0.5$, $S = 0.2$,

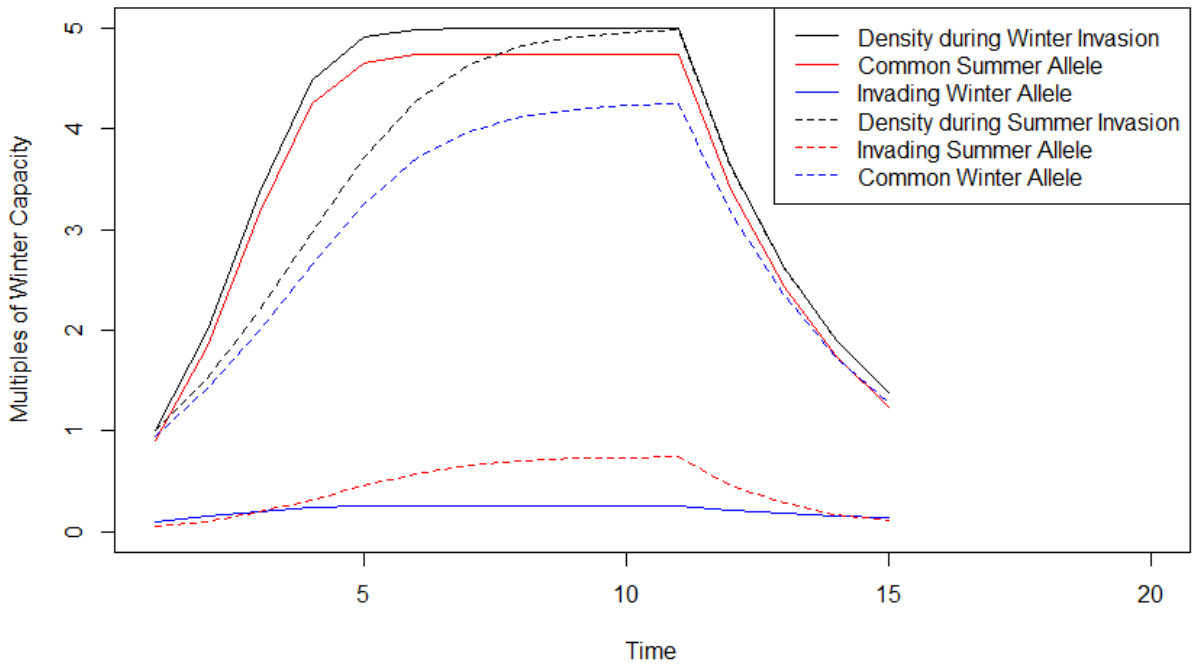

Figure 3.1: Full lines show densities of summer allele, winter allele and total density during a winter invasion. Due to the summer allele being common, capacity is reached quickly and its relative advantage is only present for a short period of time. Dashed lines show a summer invasion. Due to the winter allele being common, summer capacity is not reached for long and the summer allele carries the relative advantage.

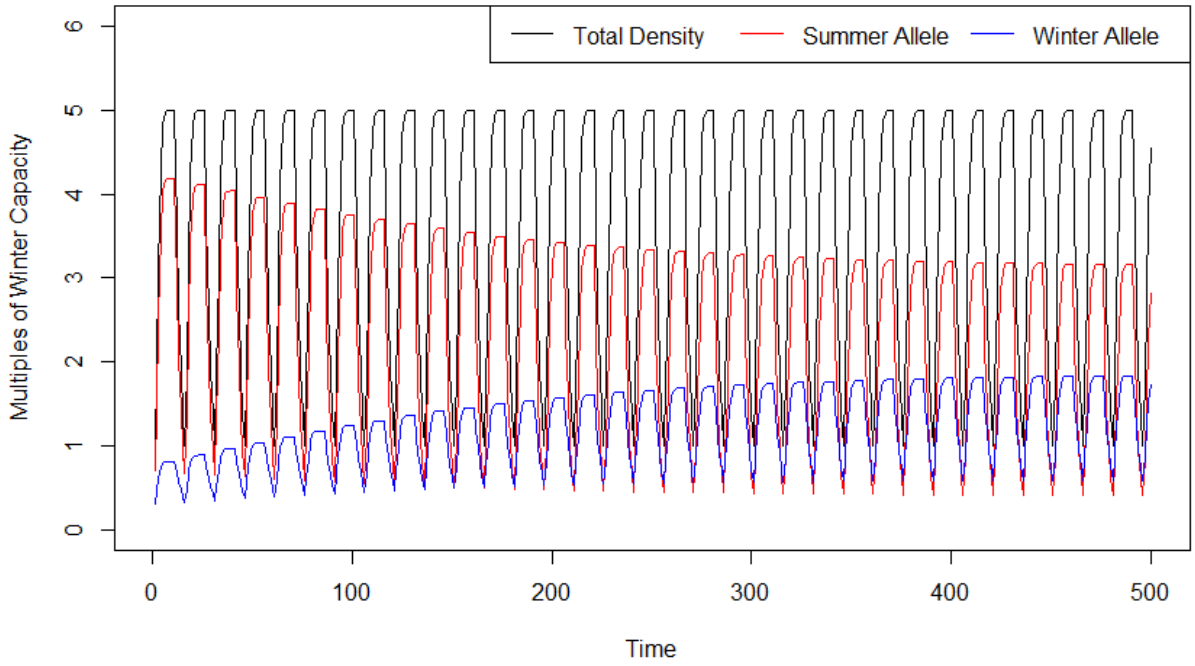

Figure 3.2: A surviving polymorphism with the starting parameters $r_A = 0.9$, $r_B = 0.5$, $S = 0.2$, $t_s = 10$, $t_w = 5$ and $K_s = 5K_w$.

$t_s = 10$, $t_w = 5$ and the summer capacity is 5 times the winter capacity. For additional information on the accuracy of these criteria consult Appendix A.

One can extend this model by making the selective advantage depend on the time t. Then one gets the criteria:

$$1 < \prod_{t=1}^{t_w} (1 + s(t))^{-1} * \left(\frac{y_{s,t_s}}{K_w} \right)^{(\frac{r_A}{r_B} - 1)}, \tag{3.11}$$

and

$$1 < \prod_{t=1}^{t_w} (1 + s(t)) * \left(\frac{x_{s,t_s}}{K_w} \right)^{(\frac{r_B}{r_A} - 1)}. \tag{3.12}$$

If one assumes that capacity is approximately reached during summer, which is necessary for survival of polymorphisms as well, since else growth rates do not change during the constant length of the summer, one gets:

$$1 < \prod_{t=1}^{t_w} (1 + s(t))^{-1} * \left(\frac{K_s}{K_w}\right)^{(\frac{r_A}{r_B} - 1)}, \tag{3.13}$$

and

$$1 < \prod_{t=1}^{t_w} (1 + s(t)) * \left(\frac{K_s}{K_w}\right)^{(\frac{r_B}{r_A} - 1)}. \tag{3.14}$$

3.2 Stochastic model

Given the importance of stochastic effects in population genetics [CK$^+$70], deterministic models are certainly not satisfying on their own. Hence one might want to consider the following analogue to the exponential model above. During the first season A and B alleles have Poisson distributed numbers of offspring, with a mean of e^{r_A} for individual A alleles and e^{r_B} for B alleles. Once the capacity K_s is reached or surpassed, the population is sampled according to Wright Fisher with population size K_S, where one allele has an advantage s. This happens until generation t_s is reached, where total population size starts to decline. It does so exponentially, so that at the end of the winter the total population size is K_w. During each step there is is Wright Fisher sampling with selective advantage s again. For small selection sizes one can use previous theoretical frameworks [UH11] to find probabilities of establishment for invading alleles. In particular one can derive (see materials and methods section) the general formula for fixation probabilities in an environment under periodic selection fluctuations.

$$P_{fix}(t_0) = \frac{2}{1 + G_1(t_0) + \frac{G_2(t_0)}{1 - \exp(-\int_0^n (s(\tau) + r(\tau))d\tau)}}, \tag{3.15}$$

where P_{fix} denotes the probability of eventual fixation of an allele that starts at frequency 1, t_0 is the time of the first mutation, n is the period of the selection function $s(t)$, which gives the selective advantage of the invading allele. $r(t)$ gives the growth rates of the resident, which share the same period T and

$$G_1(t_0) = \int_{t_0}^{n} (\lambda+\mu)(\tau)\exp(-\int_{t_0}^{t}(s(\tau))dt$$
$$G_2(t_0) = \exp(-\int_{t_0}^{n}(s(\tau)+r(\tau))d\tau)\int_{0}^{n}(\lambda+\mu)(\tau)\exp(-\int_{0}^{t}(s(\tau)+r(\tau))d\tau)dt. \tag{3.16}$$

Here $\lambda(\tau)$ and $\mu(\tau)$ are the periodic per capita birth and death rates of the invader.

This formula can be applied to the exponential model by making simplifications.

First we assume that all time dependent functions in the above definition are periodic. This is justified in the analysis of cases where population size is large. In such a case the probability of establishment depends on reaching only a small fraction of the total population, and hence assuming that the time dependent functions are frequency independent is warranted.

Second , we assume that the probability of establishment is equal to the probability of eventual fixation if the time dependent functions are periodic. This is again justified by the fact that once the allele is established, the probability of it dying out again is small when selective advantages do not shift with frequency.

Using this formula the probability of establishment can be calculated for our specific model. We are keeping the per capita death rates as separate constants during the initial increase the time at capacity and the decrease, named ξ_s, ξ_K and ξ_w respectively and assume that mutation happens at the beginning of the cycle to make the calculation more manageable and the solution easier on the eye, though this assumption is not necessary, see Appendix B for more extended calculations of this type. Then the probability of eventual establishment of an invading B allele in a large population is given as

$$\left(1+\frac{\frac{\xi_s}{r_B}(1-e^{\cdot t_s r_B})+\frac{\xi_K}{s}e^{-t_s r_B}(1-e^{-(t_w-t_s)s})+\frac{\xi_w}{r_w+s}e^{-t_s r_B-(t_w-t_s)s)}(1-e^{-(n-t_w)(r_w+s)})}{1-e^{-r_B t_s-s(t_w-t_s)-(s+r_w)(n-t_w)}}\right)^{-1}. \tag{3.17}$$

Here variable names are as before and r_w is the growth rate during winter and t_s and t_w are the times until summer and winter are reached respectively.

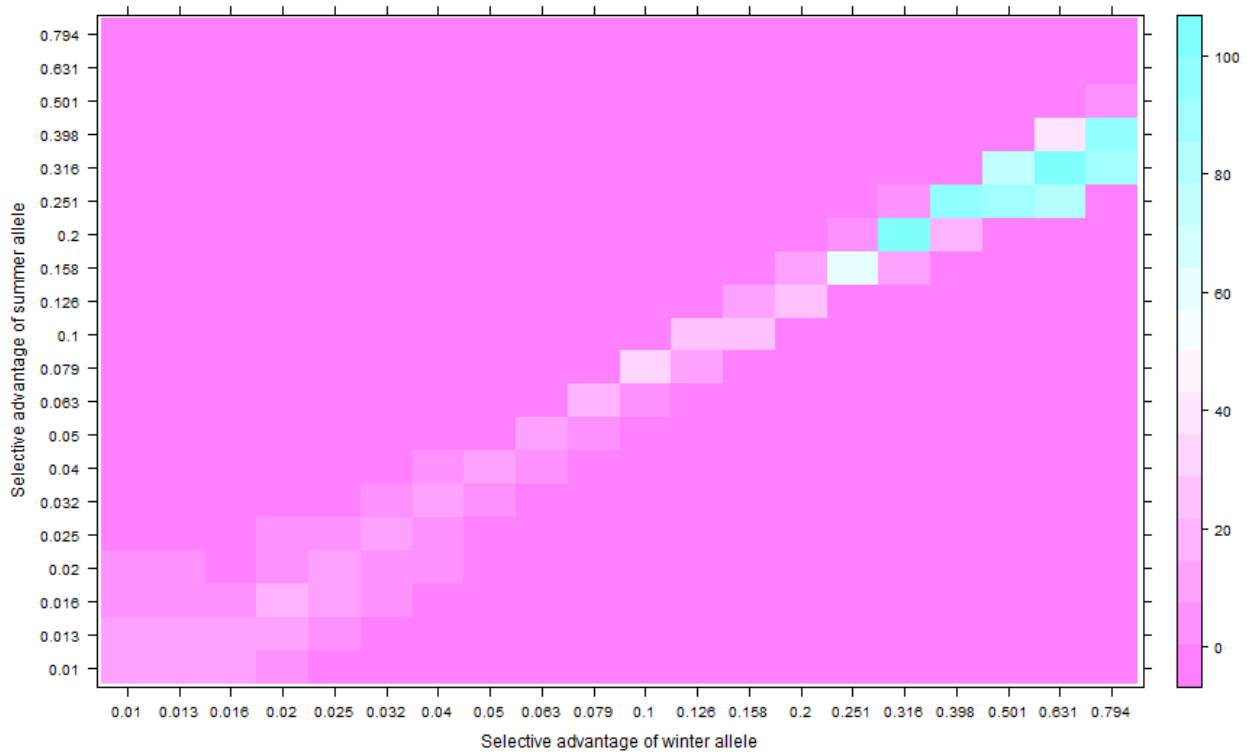

Figure 3.3: This figure shows the survival probability in a stochastic simulation with the following parameters: $K_s = 10000$, $K_w = 100$, basic growth rate of allele B at beginning of summer is 2, that of allele A is $2 * e^s$ where s is the current advantage of allele A, simulated for 100 year cycles.

3.3 Stochastic simulation

To further understand model behaviour, simulations where conducted. The corresponding source code is in Appendix C. In summer individuals of both alleles replicate according to a Poisson distribution with different means until summer capacity is reached. At capacity they are then sampled according to the Wright Fisher model with population size equal to summer capacity, until summer time is over. Then they are sampled according to Wright Fisher with exponentially decreasing capacity. One allele has a higher growth rate at the beginning of summer, the other one has a selective advantage during Wright Fisher sampling. Survival probability for a parameter choice is shown.

Starting at intermediate values, the probability of maintenance for 100 year cycles or 2000 generations is given in figure 3.3.

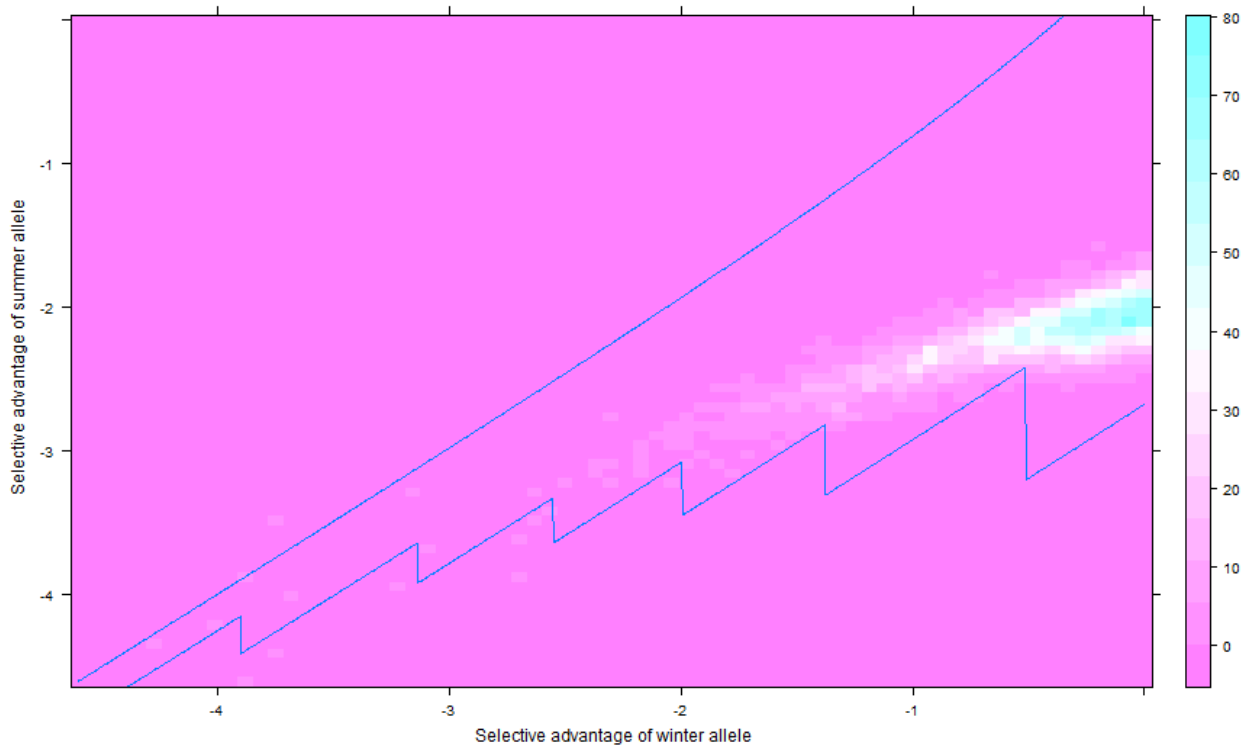

Figure 3.4: This Figure shows the survival probability of alleles in a scenario with a mild winter and low population size. Parameters are: $r_B = \log(1.1)$, $n = 16$, $t_s = 10$, $K_w = 100$, $K_s/K_w = 2$, simulated for 100 year cycles. Blue lines indicate the area where mutual invasion is predicted by the deterministic criteria. Axis are logarithmic.

Overall one can conclude that with this parameter constellation, survival is unlikely, since it depends on a very well calibrated ratio of selective advantages.

I then used the conclusions of subsection 1.2 to find more tolerant parameters. When one starts with a winter capacity of 100 and simulates 100 years, drift is too strong and only a few parameter combinations survive, see figure 3.4.

Blue lines are the boundaries of the area predicted to enable coexistence by the analytic dynamics.

Larger values for the winter capacity however lead to much more stable coexistence. These are shown in figure 3.5 and figure 3.6.

We see progressively better agreement with theory and very large areas where coexistence is possible. To gain a comparison with situations sporting a harsh winter I used the

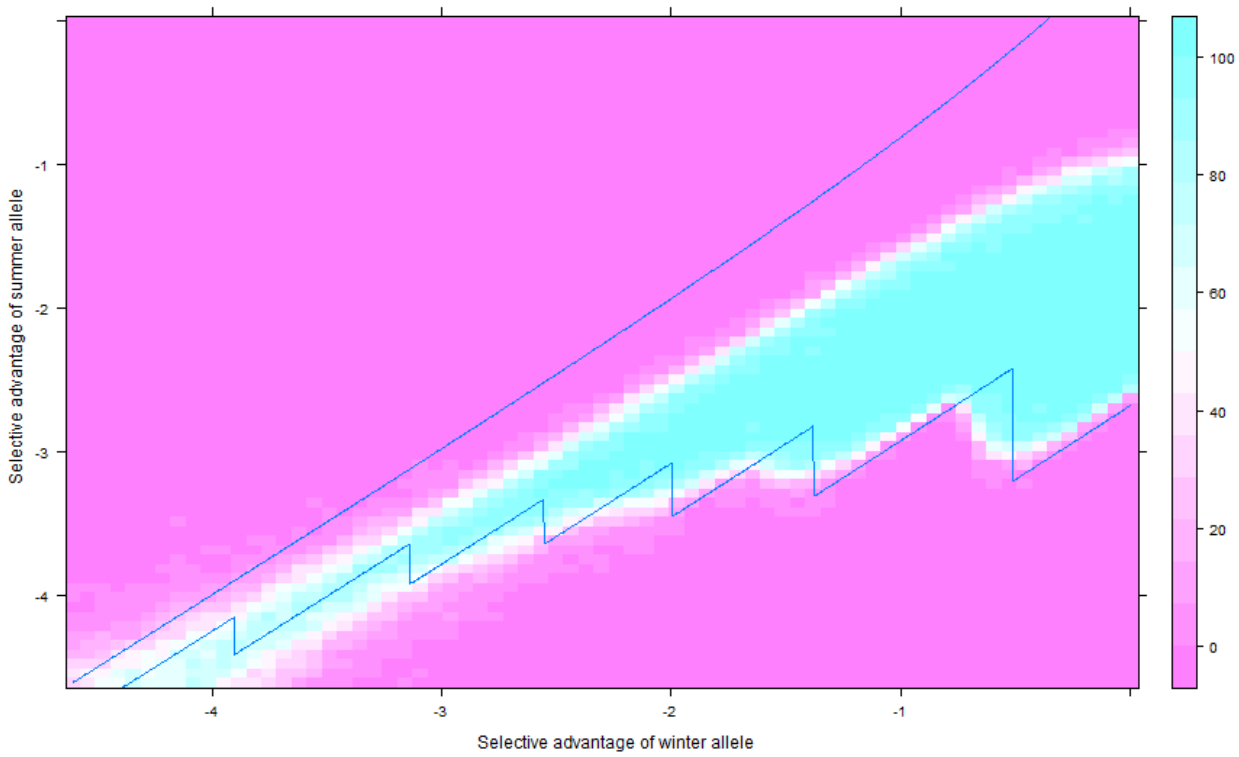

Figure 3.5: This Figure shows the survival probability of alleles in a scenario with a mild winter and medium population size. Parameters are: $r_B = \log(1.1)$, $n = 16$, $t_s = 10$, $K_w = 1000$, $K_s/K_w = 2$, simulated for 100 year cycles. Blue lines indicate the area where mutual invasion is predicted by the deterministic criteria. Axes are logarithmic.

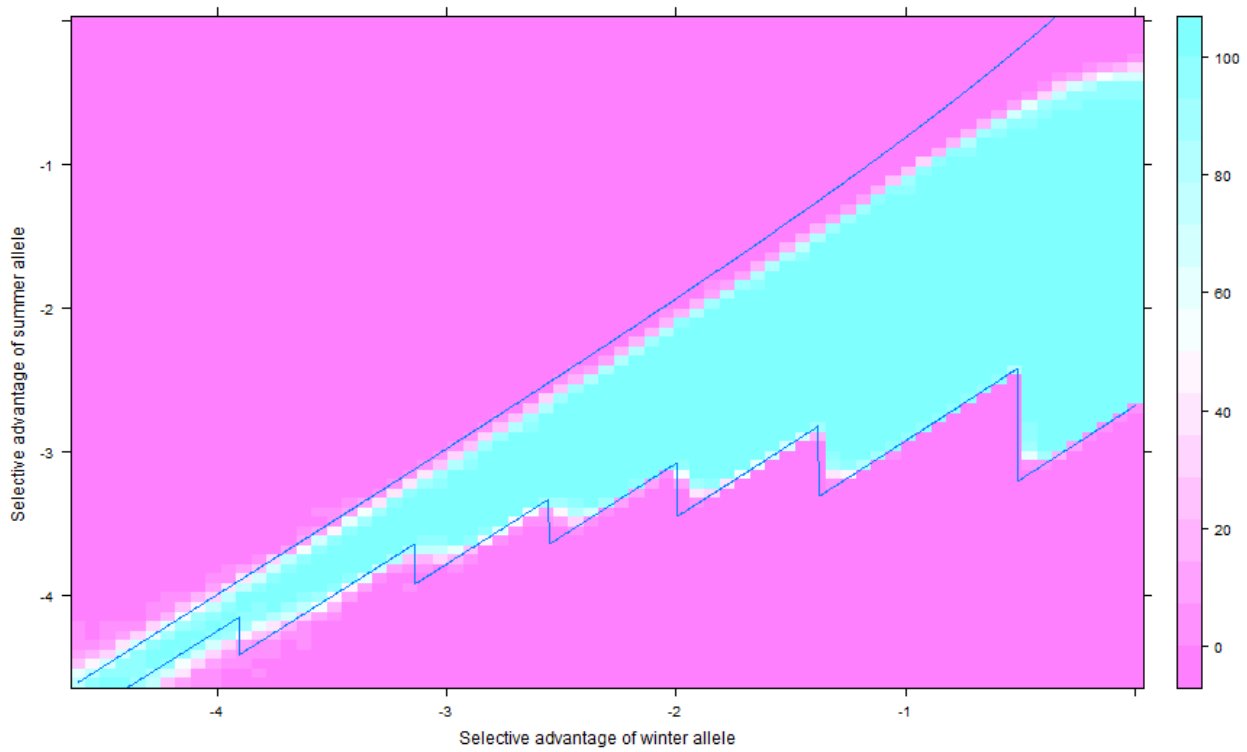

Figure 3.6: This Figure shows the survival probability of alleles in a scenario with a mild winter and large population size. Parameters are: $r_B = \log(1.1)$, $n = 16$, $t_s = 10$, $K_w = 10000$, $K_s/K_w = 2$, simulated for 300 year cycles. Blue lines indicate the area where mutual invasion is predicted by the deterministic criteria. Axes are logarithmic.

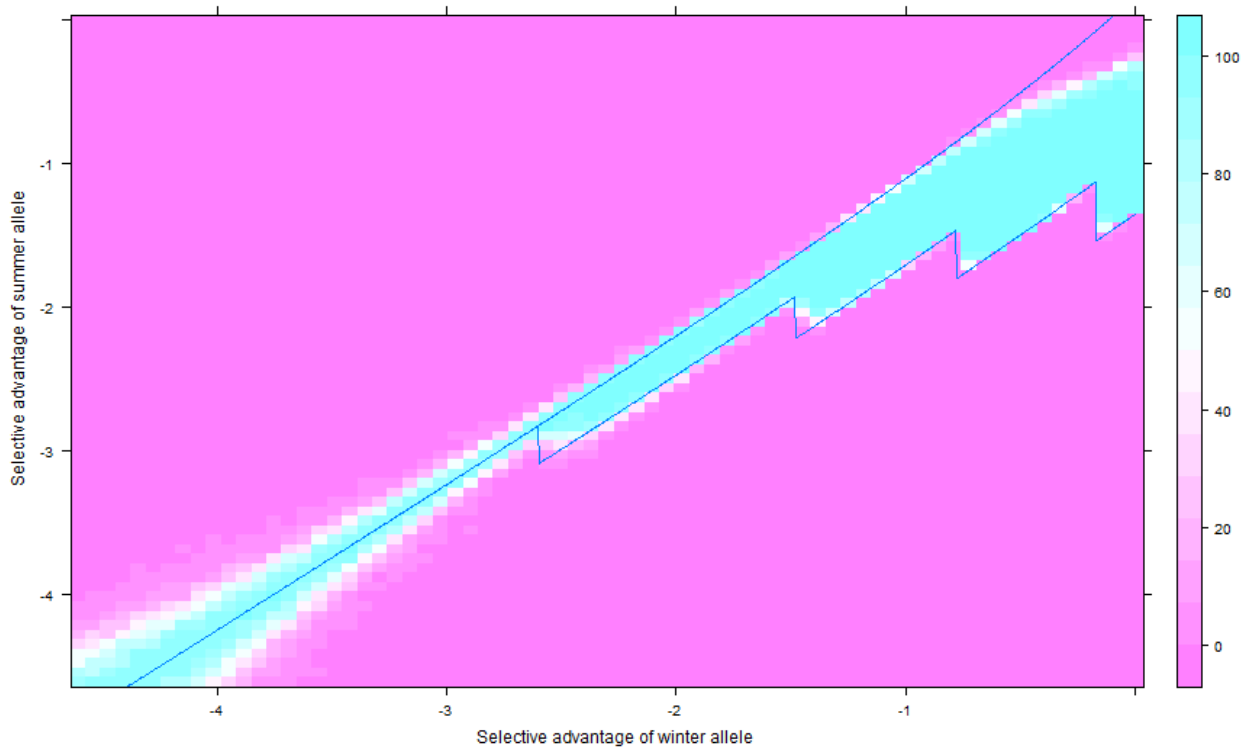

Figure 3.7: This Figure shows the survival probability of alleles in a scenario with a harsh winter and medium population size. Parameters are: $r_B = \log(1.1)$, $n = 16$, $t_s = 10$, $K_w = 1000$, $K_s/K_w = 2$, simulated for 100 year cycles. Blue lines indicate the area where mutual invasion is predicted by the deterministic criteria. Axes are logarithmic.

same winter capacities and lengths of simulations for starting parameters: $K_s/K_w = 100$, $r_B = \log(2)$, gaining figure 3.7 and figure 3.8

To test whether deterministic predictions where applicable in the limit case I simulated a very large population with 1000000 winter capacity and 2000000 summer capacity for 10000 year cxcles. The blue lines indicate the boundaries of the area in which deterministic analysis predicted mutual invasion. One sees good agreement with theory in figure 3.9.

Whether stochastic simulations were in agreement with theoretical predictions of section 3.2 was investigated as well. For varying selection strengths between -0.1 and 0.1 in winter and summer the invasion of a single allele at the beginning of winter was simulated. r_A was chosen as $\log(1.5)$, while K_w was equal to 10000 and $K_s = 50000$. ξ was set to 0.5 in all phases. Invasion probabilities of can be seen in figure 3.10. These can be

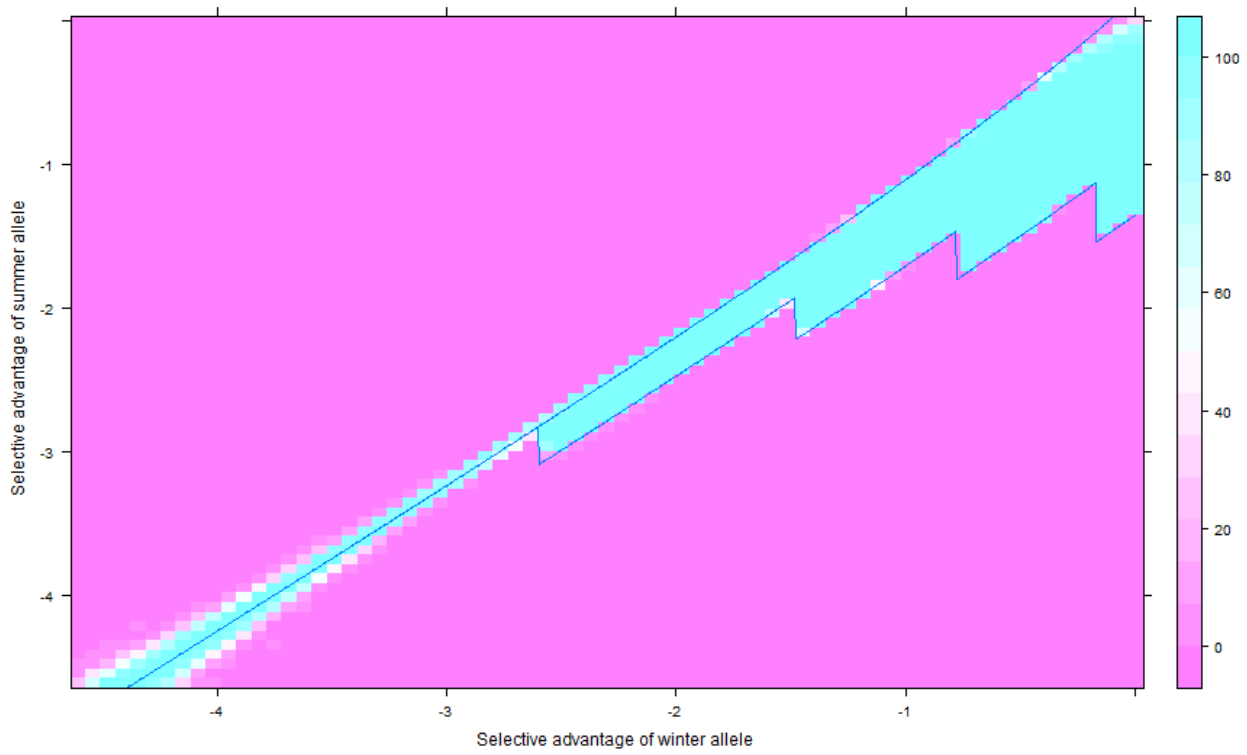

Figure 3.8: This Figure shows the survival probability of alleles in a scenario with a harsh winter and large population size. Parameters are: $r_B = \log(1.1)$, $n = 16$, $t_s = 10$, $K_w = 10000$, $K_s/K_w = 2$, simulated for 300 year cycles. Blue lines indicate the area where mutual invasion is predicted by the deterministic criteria. Axes are logarithmic.

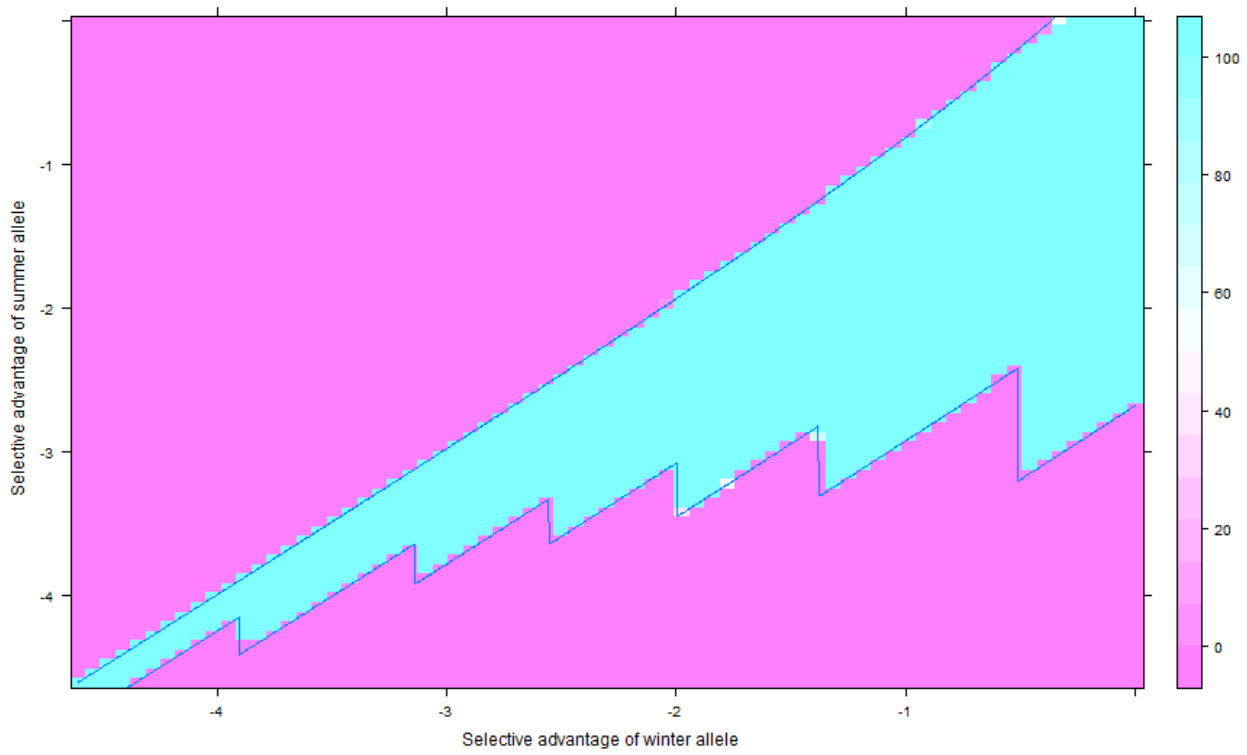

Figure 3.9: This Figure shows the survival probability of alleles in a scenario with a mild winter and a very large population size. Parameters are: $r_B = \log(1.1)$, $n = 16$, $t_s = 10$, $K_w = 1000000$, $K_s/K_w = 2$, simulated for 100000 year cycles. Blue lines indicate the area where mutual invasion is predicted by the deterministic criteria. Axes are logarithmic.

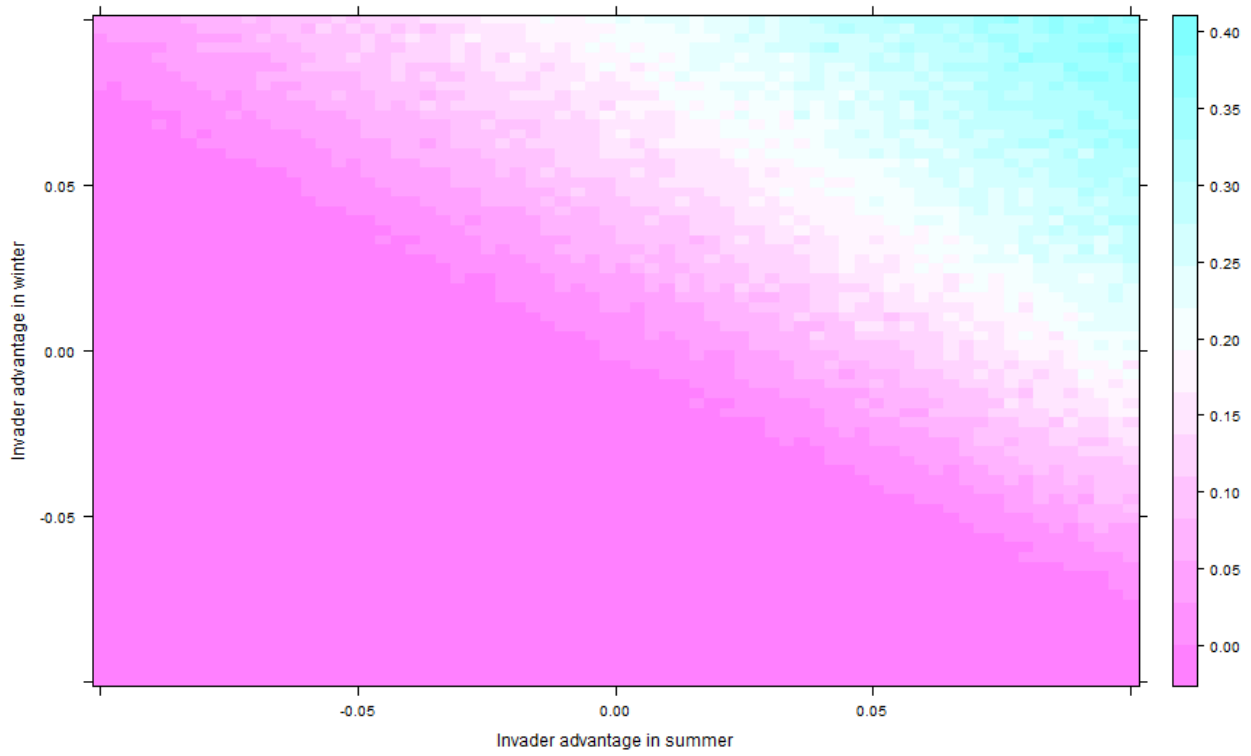

Figure 3.10: Establishment probabilities of an allele under temporally fluctuating selection. Parameters are: $r_A = \log(1.5)$, $K_w = 10000$, $K_s = 50000$.

compared with the estimated probabilities in figure 3.11 and their absolute difference in figure 3.12.

Simulation with larger capacities lead to a similar prediction as can be seen in figure 3.14, figure 3.13 and figure 3.15. Additionally consider figure 3.16, which shows the accuracy of the predictions.

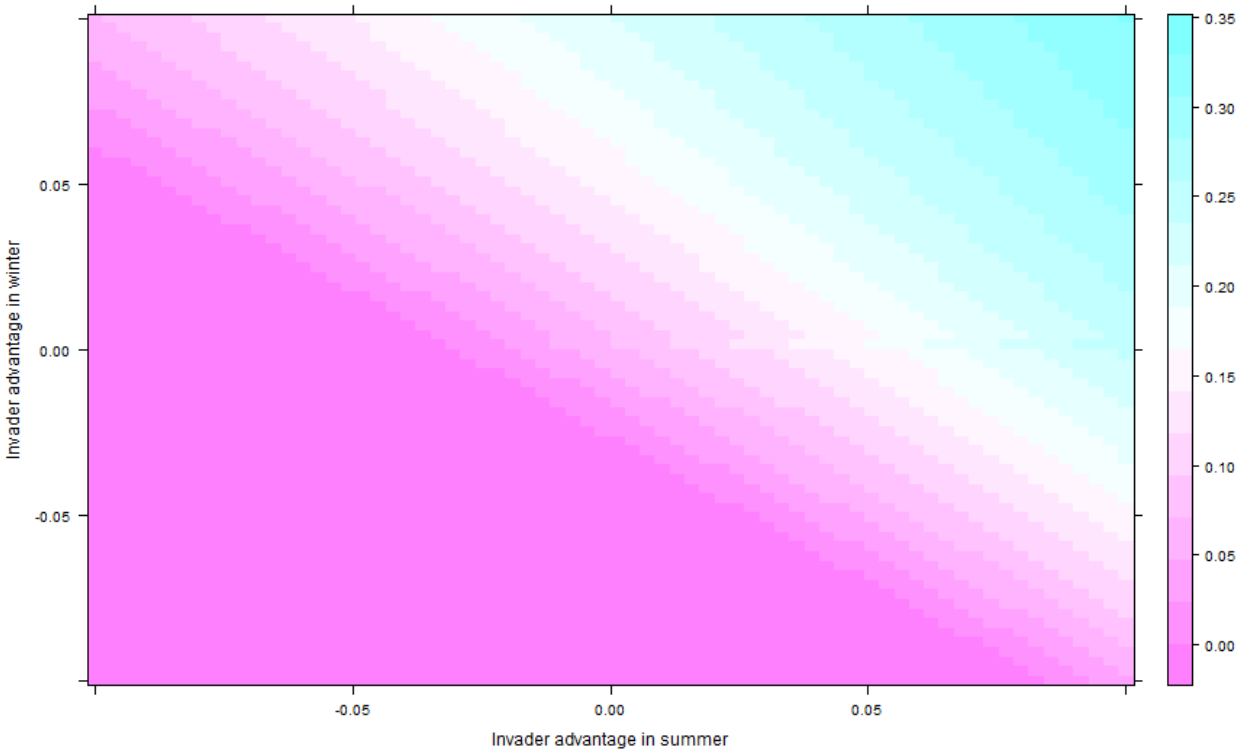

Figure 3.11: Estimated establishment probabilities of an allele under temporally fluctuating selection. Parameters are: $r_A = \log(1.5)$, $K_w = 10000$, $K_s = 50000$.

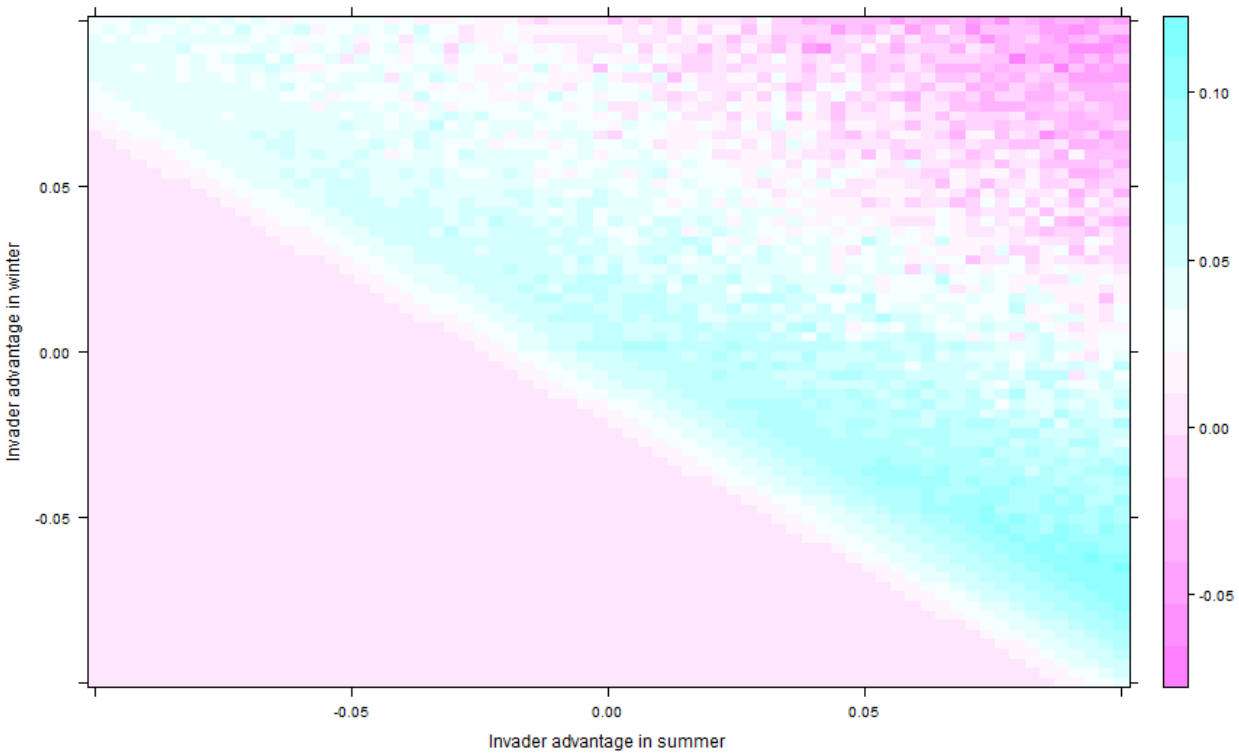

Figure 3.12: Difference between estimated establishment probabilities and simulated establishment probabilities of an allele under temporally fluctuating selection. Parameters are: $r_A = \log(1.5)$, $K_w = 10000$, $K_s = 50000$.

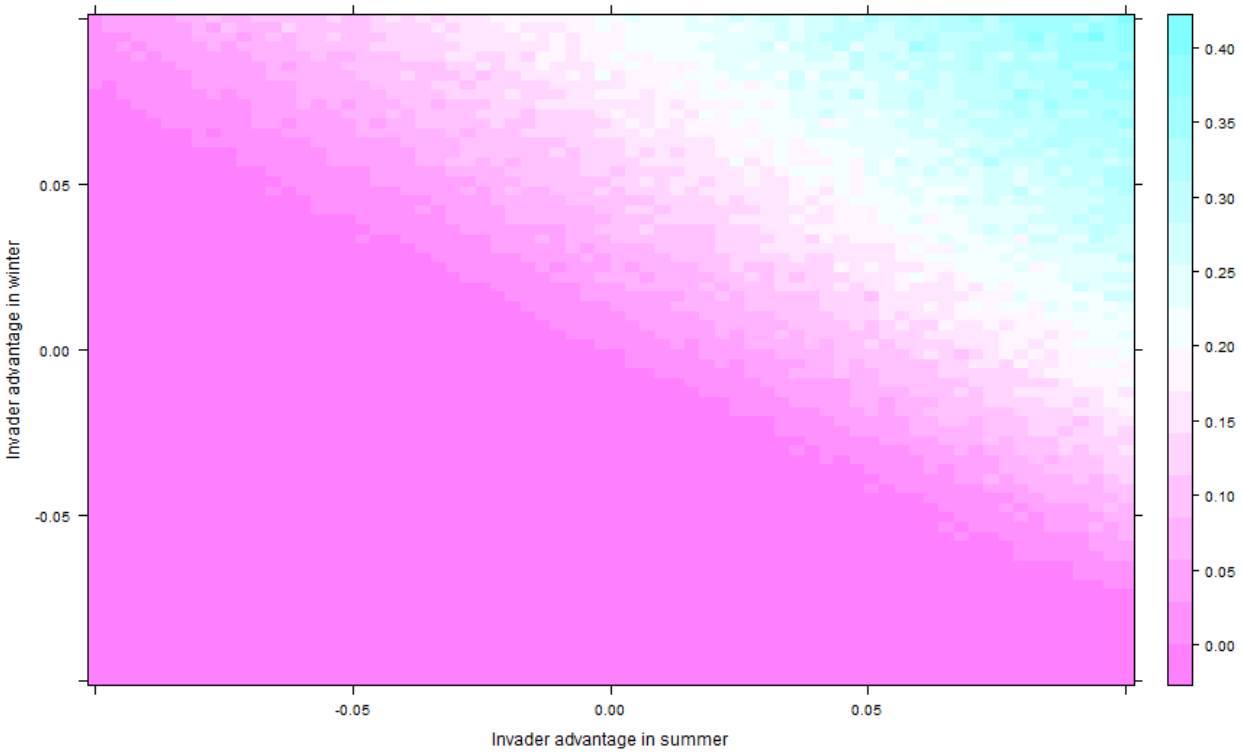

Figure 3.13: Establishment probability in a large population. Parameters are: $r_A = \log(1.3)$, $K_w = 1000000$, $K_s = 5000000$.

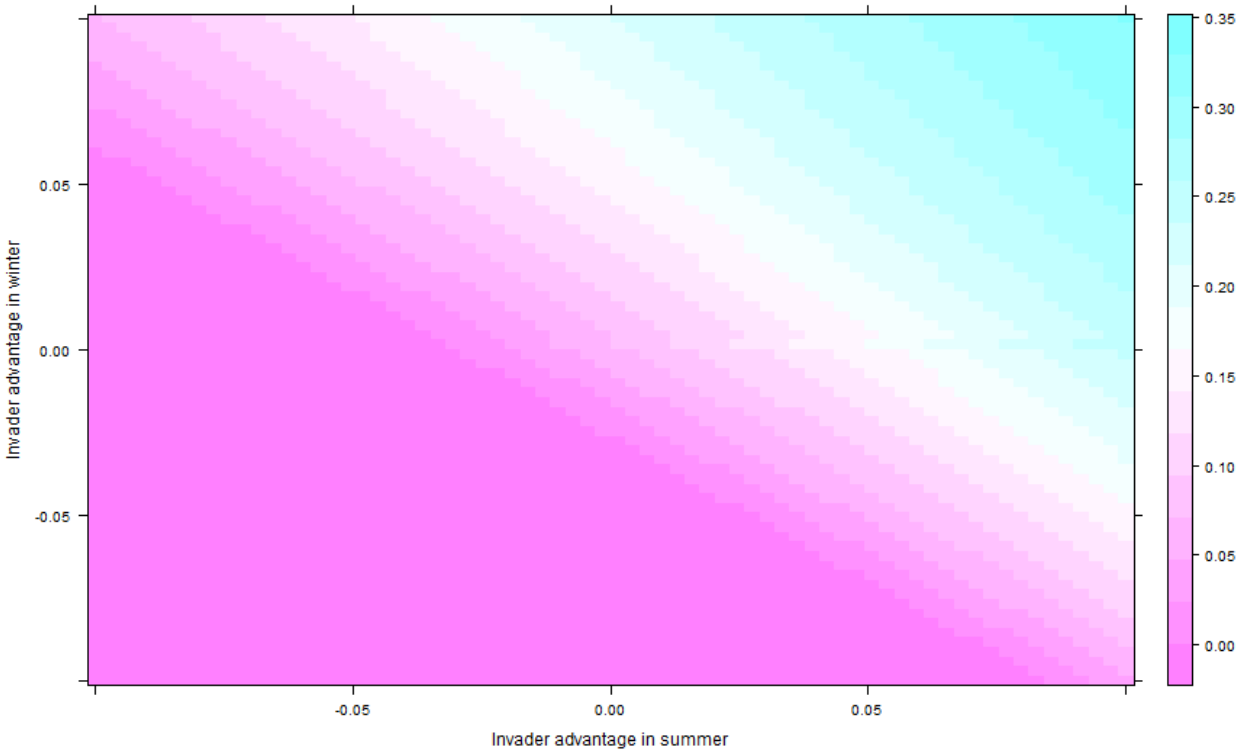

Figure 3.14: Estimated establishment probability in a large population. Parameters are: $r_A = \log(1.3)$, $K_w = 1000000$, $K_s = 5000000$.

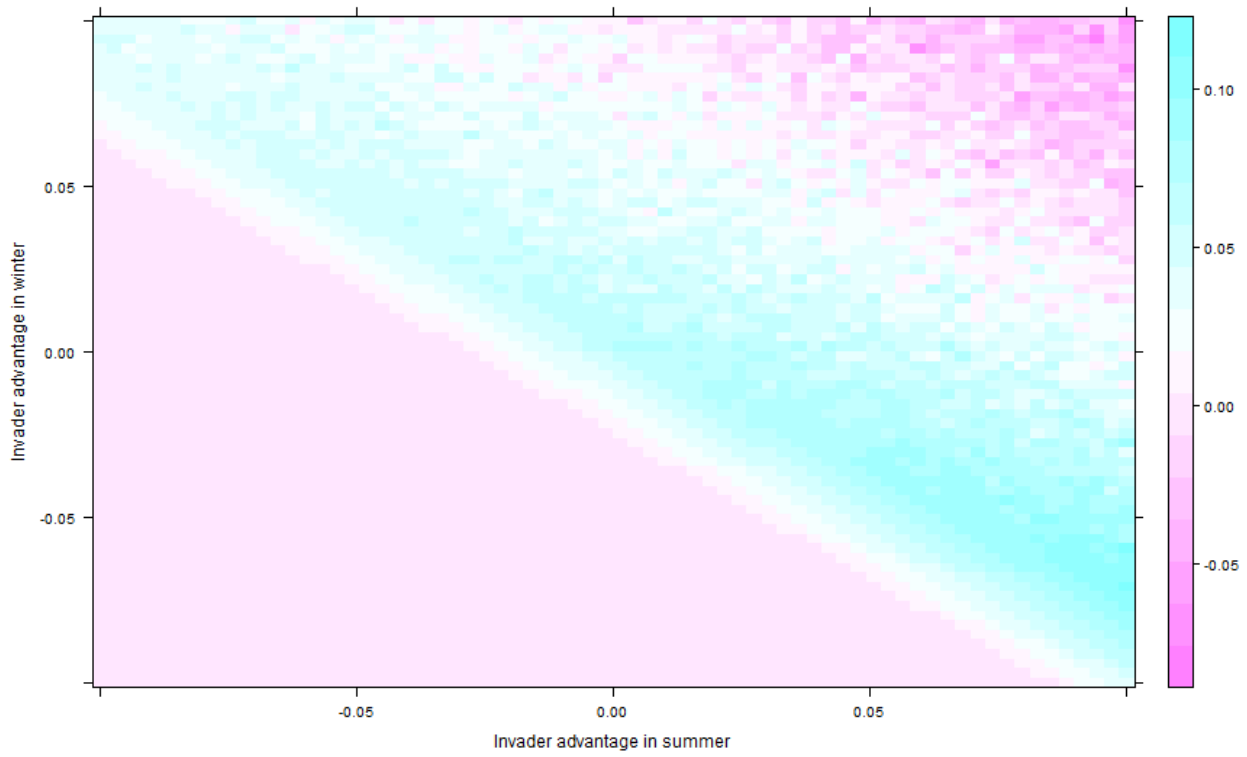

Figure 3.15: Difference between estimated establishment and simulated establishment probability in a large population. Parameters are: $r_A = \log(1.3)$, $K_w = 1000000$, $K_s = 5000000$.

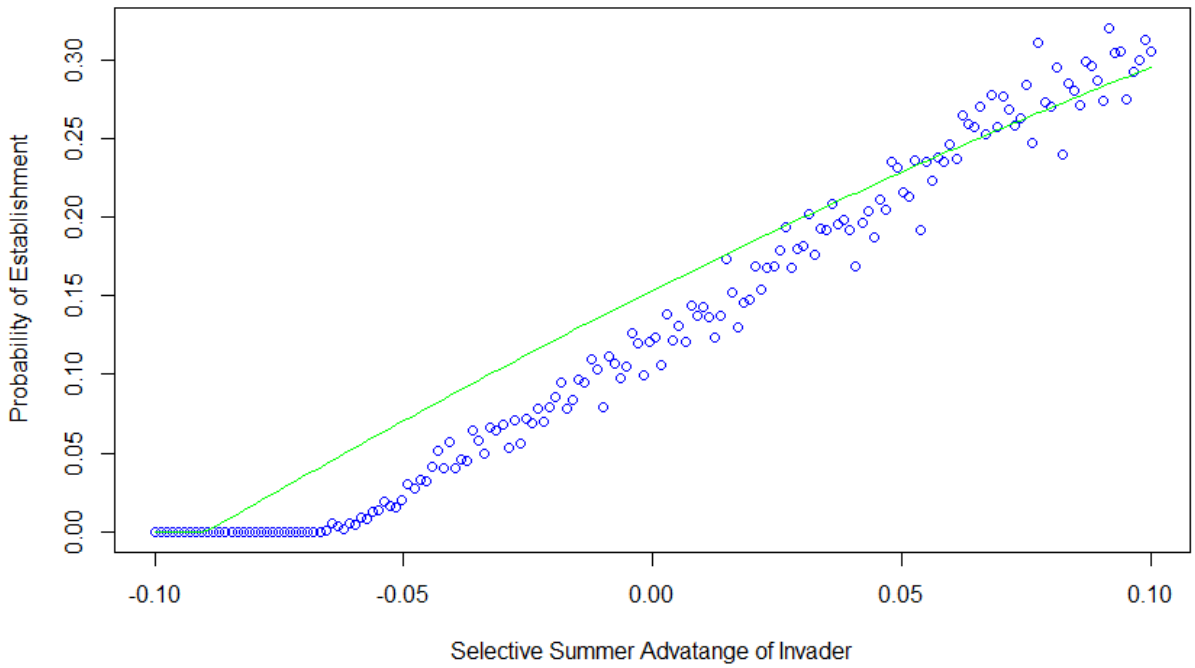

Figure 3.16: In a simulation with $K_w = 10000$, $K_s = 50000$ and $r_A = \log(1.5)$, the winter advantage of the invading allele was kept constant at $s = 0.05$, while the summer advantage varied. Blue dots give the percentage of established polymorphism, while the green line shows the theoretical prediction.

4 Material and methods

4.1 Deterministic Coexistence Criteria

4.1.1 Model with exponential growth phase

If B is rare, to increase in frequency over a cycle we need:

$$\frac{y_0}{x_0} < \frac{y_n}{x_n} \tag{4.1}$$

Now since B is rare we know that K_s is reached in approximately $t_K = \lceil \frac{1}{r_A} \log(\frac{K_s}{K_w}) \rceil \approx \frac{1}{r_A} \log(\frac{K_s}{K_w})$, where this and the following approximations holds if $t_K >> 1$. So we see

$$\frac{y_n}{x_n} = \frac{y_0}{x_0} \frac{e^{r_B t_K}}{e^{r_{A,s} t_K}} * \prod_{t=t_K+1}^{n} (1 + s(t)) \approx \frac{y_0}{x_0} (\frac{K_s}{K_w})^{\frac{r_B}{r_A}-1} * \prod_{t=t_K+1}^{n} (1 + s(t)) \tag{4.2}$$

This yields the invasion criterion 3.2 and by analogy 3.3.

4.1.2 Model with growth phase according to the Ricker model

Let allele B be rare. Then for invasion we need

$$\frac{y_0}{x_0} < \frac{y_{t_w+t_s}}{x_{t_w+t_s}} \tag{4.3}$$

Inductively we observe for winter generations

$$\frac{y_{t_w+t_s}}{x_{t_w+t_s}} = (1+s)^{t_w} * \frac{y_{t_s}}{x_{t_s}} \tag{4.4}$$

One can now observe by induction:

$$\frac{y_{t_s}}{x_{t_s}} = \frac{y_0}{x_0} * e^{(r_B - r_A)(t_s - \frac{1}{K}\sum_{k=0}^{t_s-1}(x_k+y_k))} \tag{4.5}$$

The start of the induction is true by definition. Now assume the formula is shown for $t-1$. Then we have

$$\begin{aligned} \frac{y_t}{x_t} = \frac{y_{t-1}}{x_{t-1}} \frac{e^{r_B(1-\frac{x_{t-1}+y_{t-1}}{K})}}{e^{r_A(1-\frac{x_{t-1}+y_{t-1}}{K})}} = \\ \frac{e^{r_B(1-\frac{x_{t-1}+y_{t-1}}{K})}}{e^{r_A(1-\frac{x_{t-1}+y_{t-1}}{K})}} * \frac{y_0}{x_0} * e^{(r_B-r_A)(t-1-\frac{1}{K}\sum_{k=0}^{t-2}(x_k+y_k))} = \\ \frac{y_0}{x_0} * e^{(r_B-r_A)(t-\frac{1}{K}\sum_{k=0}^{t-1}(x_k+y_k))} \end{aligned} \tag{4.6}$$

With (4.4) and 4.5, 4.3 reduces to (by cancelling y_0/x_0):

$$1 < (1+s)^{t_w} e^{(r_B-r_A)(t_s-\frac{1}{K}\sum_{k=0}^{t_s-1}(x_k+y_k))} \approx (1+s)^{t_w} e^{(r_B-r_A)(t_s-\frac{1}{K}\sum_{k=0}^{t_s-1} x_k)}. \tag{4.7}$$

where the last approximation is justified with B being the rare type. We further observe inductively that in a 1-dimensional Ricker model the following relationship holds:

$$\frac{1}{r_A}\ln(\frac{x_t}{x_0}) = t - \frac{1}{K}\sum_{k=0}^{t-1} x_k. \tag{4.8}$$

This can be seen by starting the induction a $t = 0$, where it is true and then assuming the formula holds for $t-1$. From there one calculates

$$\begin{aligned} \frac{1}{r_A}\ln(\frac{x_t}{x_0}) = \frac{1}{r_A}\ln\left(\frac{x_{t-1} * e^{r_A(1-\frac{x_{t-1}}{K})}}{x_0}\right) = \\ \frac{1}{r_A}\ln\left(\frac{x_{t-1}}{x_0}\right) + \frac{1}{r_A}\ln\left(e^{r_A(1-\frac{x_{t-1}}{K})}\right) = \\ t-1-\frac{1}{K}\sum_{k=0}^{t-2}x_k + (1-\frac{x_{t-1}}{K}) = t-\frac{1}{K}\sum_{k=0}^{t-1}x_k, \end{aligned} \tag{4.9}$$

yielding 4.8. Plugging this into (4.7) yields the criterion

$$1 < (1+s)^{t_w} * (\frac{x_t}{x_0})^{\frac{r_B-r_A}{r_A}}. \tag{4.10}$$

This leads to the invasion criteria 3.11 and 3.12.

4.2 Analytic probability of establishment

We intend to calculate the probability that once a single mutant of A or B occurs, this mutant becomes established in the population i.e reaches larger frequencies. We will follow the notation of Uecker and Hermisson [UH11]. Allele B tries to invade against common A.

Uecker and Hermisson derived that the probability of fixation for a single mutant with selective advantage $s(t)$ is

$$p_{fix} = \frac{2}{1+\int_0^\infty(\lambda+\mu)(t)\exp(-\int_0^t(s(\tau)+r(\tau))d\tau)dt} \tag{4.11}$$

Here λ is the per capita birth rate of the invading allele, μ the per capita death rate.

Let us now assume that $s(t+n) = s(t)$, $r(t+n) = r(t)$,$\lambda(t+n) = \lambda(t)$ and $\mu(t+n) = \mu(t)$

Assume now the initial mutation takes place at time t_0. So we have

$$\int_{t_0}^{\infty}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt = \int_{t_0}^{n}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))dt+ \sum_{j=1}^{\infty}\int_{j*n}^{(j+1)n}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt \quad (4.12)$$

To simplify this expression we take a look at the terms of the series:

$$\begin{aligned}
\int_{j*n}^{(j+1)n}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt = \\
\int_{j*n}^{(j+1)n}((\lambda+\mu) \\
\exp(-\int_{t_0}^{n}(s(\tau)+r(\tau))d\tau-\int_{n}^{jn}(s(\tau)+r(\tau))d\tau-\int_{jn}^{t}(s(\tau)+r(\tau))d\tau))dt = \\
\exp(-(j-1)\int_{0}^{n}(s(\tau)+r(\tau))d\tau) \\
\exp(-\int_{t_0}^{n}(s(\tau)+r(\tau))d\tau)\int_{j*n}^{(j+1)n}(\lambda+\mu)\exp(-\int_{jn}^{t}(s(\tau)+r(\tau))d\tau)dt = \\
\exp(-(j-1)\int_{0}^{n}(s(\tau)+r(\tau))d\tau) \\
\exp(-\int_{t_0}^{n}(s(\tau)+r(\tau))d\tau)\int_{0}^{n}(\lambda+\mu)\exp(-\int_{0}^{t}(s(\tau)+r(\tau))d\tau)dt
\end{aligned} \quad (4.13)$$

where we used periodicity . We observe that this expression is only dependent on the index j as an exponent of $\exp(-\int_0^n(s(\tau)+r(\tau))d\tau)$, so we see that (4.12) becomes

$$\int_{t_0}^{\infty}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt = \int_{t_0}^{n}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt+ \exp(-\int_{t_0}^{n}s(\tau)d\tau)\int_{0}^{n}(\lambda+\mu)\exp(-\int_{0}^{t}(s(\tau)+r(\tau))d\tau)dt * \sum_{j=0}^{\infty}(\exp(-\int_{0}^{n}(s(\tau)+r(\tau))d\tau))^{j} \quad (4.14)$$

The infinite series has now been reduced to a geometric series. The criterion for this sum to converge is that $\int_0^n(s(\tau)+r(\tau))d\tau > 0$, i.e. that the invading allele has a mean advantage over the period. Using the standard formula for the summation of geometric series we gain:

$$\int_{t_0}^{\infty}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt = \int_{t_0}^{n}(\lambda+\mu)\exp(-\int_{t_0}^{t}(s(\tau)+r(\tau))d\tau)dt+ \frac{\exp(-\int_{t_0}^{n}(s(\tau)+r(\tau))d\tau)\int_{0}^{n}(\lambda+\mu)\exp(-\int_{0}^{t}(s(\tau)+r(\tau))d\tau)dt}{1-\exp(-\int_{0}^{n}(s(\tau)+r(\tau))d\tau)} = G_1(t_0)+\frac{G_2(t_0)}{1-\exp(-\int_{0}^{n}(s(\tau)+r(\tau))d\tau)} \quad (4.15)$$

Now putting all together we have

$$P_{fix}(t_0) = \frac{2}{1+G_1(t_0)+\frac{G_2(t_0)}{1-\exp(-\int_0^n(s(\tau)+r(\tau))d\tau)}} \quad (4.16)$$

5 Discussion

The central result of this thesis is that maintenance of clonal polymorphisms is possible in an ecologically relevant models with temporally fluctuating selection. The mechanism behind coexistence is due to bounded population size moderating the time where there is differential growth. The basic model consists of two alleles competing during an initial growth phase until a capacity is reached. Those alleles reproduce with different rates so time until capacity is reached depends on frequency of the alleles, leading to negative frequency dependent selection, i.e. the less frequent an allele, the higher its mean fitness is.

The most elementary implementation of this mechanism is a model where the initial growth is modelled exponentially. For such a model exact criteria for mutual invasion can be derived. Analysing these criteria leads to the finding that keeping selection and time of the winter allele to reach fixation constant, low growth rates are more important to ensuring survival than a large difference between summer and winter. This implies that the mechanism for survival is not strongly tied to large differences in capacities between seasons, since a smaller difference between capacities can be compensated by lower growth rates. In fact one can imagine that the lack of competition after a harsh winter increases growth rates due to lack of competition, counter balancing the effect of large capacity differences. One can potentially view the finding of preservation of polymorphism in African populations of Drosophila[BBO$^+$14] in this light. Even small capacity differences between seasons are enough to prevent extinction of alleles if the growth rates are low enough. Crucially, if this is to be the case, growth rates during expansion need to be relatively lower in areas with mild winters as compared to other areas, though they do not need to be absolutely low.

However, while being analytically tractable a model with an exponential increase has a discontinuity in growth once it reaches capacity, where the formerly exponential growth imme-

diately goes to zero. This is unrealistic, since one would assume growth in the real world to slow down once capacity is approached due to competition being stronger.

One can take this into account by modelling the increase with the Ricker model. The Ricker model was originally derived for fisheries to model density dependent growth [Ric54]. The Ricker model leads to the growth rates adjusting when capacity is approached instead of them abruptly changing. While being realistic in this respect, the Ricker model suffers from two potential drawbacks. First, it cannot be solved analytically. However, as can be seen in the results section, precise approximation criteria can be derived that can be used to determine whether a particular parameter distribution allows for coexistence of alleles. These criteria are very similar to the criteria derived for the exponential model, making the two models easily comparable. The second potential drawback is the fact that the Ricker model may behave chaotically if growth rates are too high. So while the Ricker model may be used to model initial growth, one has to be careful about how large the initial growth rate is. See further discussion in section 5.4.

Both deterministic models make the same assumption for winter, namely that the combined frequency is set to a fixed winter capacity at the end of winter. While naive models with additionally variable winters fail (see section 5.3), it is indeed possible to have models with more complicated winter. Several of these models are discussed in Appendix A.

5.1 Diploidy

A question that naturally arises, is whether the findings of the result section, which concern themselves with haploids, can be generalized to diploids. Fortunately this can be answered in the affirmative. Consider a case with multiplicative selection, i.e. type AA individuals have offspring alleles with Malthusian rate $2r_A$ in summer and have no advantage once at capacity, AB individuals produce offspring alleles with Malthusian rate $r_A + r_B$ and have advantage $(1 + s)$ and finally BB individuals produce with rate $2r_B$ in the summer and have advantage $(1 + s)^2$.

Then for B to increase in frequency when only A is present, we just have to compare the dynamics of the heterozygotes and the AA type, since the BB types will be too rare to matter during initial invasion and the heterozygotes will be rare compared to the

homozygotes making their growth irrelevant to the growth of A. To see whether B can invade we consider the relative advantage that a heterozygote has during summer, namely $\frac{e^{(r_B+r_A)}}{e^{2r_A}} = e^{r_B-r_A}$ and the relative advantage it has during winter, namely $(1+s)$ and see that they are identical to the advantages a single haploid B allele has during invasion against a common haploid A allele.

This means so long as the dynamics of the A allele are unchanged the invasion criterion remains the same. For this to be true we need to check when capacity is reached in the same time. Since heterozygotes are rare, they do not contribute to capacity and only the homozygotes need to be considered, which reproduce completely analogously to the haploid case.

If on the other hand A were to invade its relative advantage during summer would be $\frac{e^{(r_A+r_B)}}{e^{2r_B}} = e^{r_A-r_B}$ and once at capacity $\frac{(1+s)}{(1+s)^2} = (1+s)^{-1}$, which is again identical to the relative advantage enjoyed by A during a haploid invasion. By the analogous argument the criteria for coexistence are hence identical.

The same analysis lets one derive invasion criteria in the Ricker model for diploids, which are again identical.

5.2 Comparison to marginal overdominance

Several mechanisms have been proposed on how temporally fluctuating selection might preserve polymorphism. One of these is marginal overdominance [Dem55]. One speaks of marginal overdominance when two alleles in diploids achieve overdominance over a period of fluctuating selection, without being overdominant at any given period of time. For a simple model, consider the alleles A and B where the during one generation the genotypes AA, AB and BB have relative fitnesses $(1+s)$,$(1+s/2)$ and 1 respectively and during the next generation 1 ,$(1+s/2)$ and $(1+s)$, with both selection scenarios alternating. Then the fitness of AA and BB types over two generations is $(1+s)$, but the fitness of AB types is $(1+s/2)^2 = 1+s+\frac{s^2}{4} > 1+s$. So the fitness of the heterozygote is higher than that of the homozygotes if taken over both generations and this despite the fact that in each individual generation fitness is additive. This mechanism crucially depends on diploidy, whereas the mechanism discussed in this thesis does not, since only haploidy is required.

Further if one is to analyse the diploid case of the above models, one sees that the heterozygote will always be intermediate in geometric mean fitness. To see this assume that summer capacity is reached in time t_s. Then heterozygotes produce offspring alleles with the rate $e^{r_A+r_B}$ during the increase and homozygotes with the rates e^{2r_A} and e^{2r_B} respectively. Over t_s generation this leads to a total increase of $e^{(r_A+r_B)t_s}$, $e^{2r_At_s}$ and $e^{2r_Bt_s}$. In the second phase of length t_w an analogous argument yields relative fitnesses $(1+s)^{2t_w}$, $(1+s)^{t_w}$ and 1 for the BB, AB and AA genotype respectively. Let us now assume that the fitness over the year cycle of the BB homozygote is higher than the AA homozygote. This means

$$e^{2r_Bt_s}(1+s)^{2t_w} > e^{2t_sr_A}. \tag{5.1}$$

Then immediately by finding the square root

$$e^{r_Bt_s}(1+s)^{t_w} > e^{t_sr_A}. \tag{5.2}$$

Hence

$$e^{2r_Bt_s}(1+s)^{2t_w} > e^{t_sr_A}e^{r_Bt_s}(1+s)^{t_w}, \tag{5.3}$$

which is equivalent to the heterozygotes having lower fitness than BB homozygotes. The converse follows completely analogously if AA has higher mean fitness than BB.

5.3 Additional phases of variable length

In their paper [YD13], Yi and Dean use two consecutive environments with each different environment giving one of the clones an advantage in the form of a higher exponential growth rate. To see why a similar model cannot preserve polymorphisms in ecological scenarios, consider the following model. There are two consecutive seasons with capacities K_s and K_w. Label the populations A and B with respective exponential growth rates $r_{A,s}$ and $r_{B,s}$ in summer as well as $r_{A,w}$ and $r_{B,w}$ in winter. Seasons end once capacity is reached. Noting that the times to reach capacity in winter and summer respectively are

$\frac{1}{r_{B,s}} \log(K_s/K_w))$ and $\frac{1}{r_{B,w}} \log(K_w/K_s)$ the criterion for A to invade from low frequencies is

$$1 < \exp((r_{A,s} - r_{B,s})\frac{1}{r_{B,s}} \log(K_s/K_w)) + (r_{A,w} - r_{B,w})\frac{1}{r_{B,w}} \log(K_w/K_s)) = \\ = (\frac{K_s}{K_w})^{\frac{r_{A,s}}{r_{B,s}} - \frac{r_{A,w}}{r_{B,w}}} \tag{5.4}$$

That is incompatible with the analogous criterion for B. Modifications of this model using Ricker models lead to a similar result, see Appendix A. To explain this counter intuitive result, consider first invasion of an allele with summer advantage. Because the winter allele is common summers are long in the sense that capacity takes a long time to reach. From this the summer allele has an additional advantage during summer. But during winter capacity is reached slowly since the winter population does not sink quickly and during this long winter the summer allele has a relative disadvantage.
If on the other hand the winter allele tries to invade, the summers are short, since the common summer allele can reach capacity quickly, while the winters are short as well, because the common summer alleles die off. This means the phases are either both short or both long, causing the absence of frequency dependent selection.

More generally this reasoning implies that models with two seasons of variable length are at a disadvantage compared to models with only one such season when it comes to preserving genetic diversity, since the additional season negates the effect of the first such season. As one might expect adding further seasons may again be beneficial to survival, see Appendix A.

5.4 Approximation results in Ricker models

Since the Ricker model with winter is analytically intractable, the accuracy of the approximate criterion is of interest.The general finding is that the criteria discussed in the previous section and the appendix A are very accurate, as long as the growth rates are low, i.e. r_A and r_B are smaller than 4 and there are enough generations in order to reach capacity. The second of these assumptions is explicit in the approximation. If the number

of generations is lower than that the Ricker model behaves similar to an exponential model until summer ends. Since there is no large slow down in growth close to capacity, there can be no frequency dependent selection and one of the alleles wins. If growth rates are too large one observes chaotic behaviour, with one allele eventually going extinct.

The Ricker models discussed above and in appendix A allow for generalization. In particular the capacity functions can vary to an extent with time and the approximation results still hold, if at the end of each season both allele densities approach K_s and K_w respectively. To see this we observe that an analogue to (4.8) still holds for a one dimensional Ricker model with growth rate r and time dependent capacity $K(t)$ namely

$$\frac{1}{r}\log\left(\frac{x_n}{x_0}\right) = n - \sum_{l=0}^{n-1}\frac{x_l}{K(l)} \tag{5.5}$$

If x_n approaches K_s and $x_0 \approx K_w$ this yields the same criterion as discussed previously in section 3.1.2.

At this point one will have to raise a word of caution with regards to Ricker model variants where there is a winter and capacity is reached from above, since if the winter capacity is much smaller than the summer capacity, the exponent in the Ricker model becomes a large negative number and the population size collapses instantaneously. This is generally an undesirable artefact of the Ricker model, so winter should only be modelled with the Ricker model if K_w is not much smaller than K_s.

5.5 Stochastic model behaviour

To further explore model behaviour a stochastic version was devised. The mean number of offspring during the initial increase is here again given exponentially, but instead of a fixed number of offspring, each alleles offspring is giving by a Poisson distribution. After capacity is reached or overshot, Wright Fisher sampling happens with the capacity as population size. At a fixed number of generations population size decreases exponentially towards winter capacity where we have Wright Fisher sampling again. Since this model is analytically complicated, simulations were performed.

Generally, low population sizes lead to the extinction of alleles due to stochastic effects[KO69]. In concord with this standard result, we find that small population sizes lead to quick extinctions despite the selective mechanism being in place, see figure 3.4.

Larger sample sizes however lead to increasingly consistent survival of polymorphisms, as seen in the results section. Note here that the effective population size is given by the harmonic mean of the population sizes and is hence dominated by the low points in the population, which means that it is close to the winter capacity. Together with the fact that a year is modelled to have 16 generations the mechanism results in survival that is way beyond fixation times for drift in larger populations.

One distinctive feature is the particular shape the graph of the area of survival takes in the graphs. This is an artefact of the discrete generations assumed in the model. When certain thresholds are passed by the selective advantage of the summer allele, there is a jump in the number of generations needed to reach capacity causing the "spikes" in the graph.

Besides simulation, derivation of analytic results was also possible by building on work by Uecker and Hermisson [UH11]. The formula are unwieldy, (see Appendix B) but they allow for moderately precise prediction of establishment probabilities once population sizes are large enough.

A Appendix

A.1 Exponential model with one fixed time

Alleles A and B compete under the following conditions: There is exponential growth with growth rates $r_{A,S}$ and $r_{B,S}$ until a fixed density $1/f$ is reached within the time t_s. This phase is referred to as summer. Then there is exponential growth for a fixed time t_w with growth rates $r_{A,S}$ and $r_{B,S}$. This phase is referred to as winter. Their frequencies are then normalized again and a new summer winter circle (year) starts.
$d_{A,S} = r_{A,S} * t_s / log_2(e)$ and $d_{A,W} = r_{A,W} * t_w / log_2(e)$ are the number of doublings allele A receives over summer and winter $d_{B,W} = r_{B,W} * t_w / log_2(e)$and $d_{B,S} = r_{B,S} * t_s / log_2(e)$ the respective doublings for B.
Then a rare allele A increases in frequency over a year, when the number of doublings by A exceeds those by B, i.e.:

$$d_{A,S} + d_{A,W} > d_{B,S} + d_{B,W} \tag{A.1}$$

or equivalently:

$$r_{A,S} * t_s + r_{A,W} * t_w > r_{B,W} * t_w + r_{B,S} * t_s \tag{A.2}$$

Since the winter has a constant time t_w we define the winter factor

$$F_W := t_w * (r_{A,W} - r_{B,W}) \tag{A.3}$$

and we rewrite the inequality as:

$$F_W + r_{A,S} * t_s > r_{B,S} * t_s \tag{A.4}$$

Since we start with a rare allele A, $1/f$ can be approximated as $2^{d_{B,S}}$. Solving for $d_{B,S}$ we gain

$$log_2(1/f) = d_{B,S} = r_{B,S} * t_s / log_2(e) \tag{A.5}$$

which yields:

$$t_s = log_e(1/f)/r_{B,S} \tag{A.6}$$

Plugging this in (A.4) and rearranging we get the condition for the rare type A to invade:

$$r_{A,S}/r_{B,S} > 1 - F_W/log_e(1/f) \tag{A.7}$$

Analogously the condition for the rare type B to invade are:

$$r_{B,S}/r_{A,S} > 1 + F_W/log_e(1/f) \tag{A.8}$$

A.2 Ricker model with winter

Model: Alleles A and B compete in the following way: Until the fixed time t they increase according to the Ricker model with capacity K and respective rates r_A and r_B. ($r_A > 0$ $r_B > 0$). Then each frequency is multiplied by the constant factors s_A and s_B respectively.

Let A be the common type with frequency x_n at the time n and B the rare type with frequency y_n.

To increase frequency after a cycle

$$\frac{y_0}{x_0} < \frac{y_t * s_B}{x_t * s_A} \tag{A.9}$$

must hold. One can now observe by induction:

$$\frac{y_t}{x_t} = \frac{y_0}{x_0} * e^{(r_B - r_A)(t - \frac{1}{K}\sum_{k=0}^{t-1}(x_k + y_k))} \tag{A.10}$$

With this the inequality reduces to (by cancelling y_0/x_0):

$$1 < \frac{s_B}{s_A} * e^{(r_B - r_A)(t - \frac{1}{K}\sum_{k=0}^{t-1}(x_k + y_k))} \approx \frac{s_B}{s_A} * e^{(r_B - r_A)(t - \frac{1}{K}\sum_{k=0}^{t-1} x_k)} \tag{A.11}$$

where the last approximation is justified with B being the rare type. We further observe inductively that in a 1-dimensional Ricker model (4.8) holds.

Plugging this (A.11) yields the criterion:

$$1 < \frac{s_B}{s_A} * (\frac{x_t}{x_0})^{\frac{r_B - r_A}{r_A}} \tag{A.12}$$

In general x may behave erratically, but in the case of x_t approximately reaching K in each circle $x_t \approx K$ and since x reached K in the previous cycle, $x_0 \approx s_A * K$. We gain:

$$s_A^{r_B/r_A} < s_B \tag{A.13}$$

And analogously, under the assumption that common B alleles approach capacity in each cycle, the criterion for invasion by A is

$$s_B^{r_A/r_B} < s_A \tag{A.14}$$

These are mutually exclusive. To test this prediction of exclusion, I did a simulation experiment where growth rates were drawn from a uniform distribution. I found no surviving polymorphisms.

This problem can be solved by normalizing the absolute frequency after each cycle. Let the notation be the same as above, except this time we normalize frequencies. Then with the same assumption of the capacity being reached in each cycle we gain the criteria:

$$1 < \frac{s_B}{s_A} * K^{\frac{r_B}{r_A} - 1} \tag{A.15}$$

$$1 < \frac{s_A}{s_B} * K^{\frac{r_A}{r_B} - 1} \tag{A.16}$$

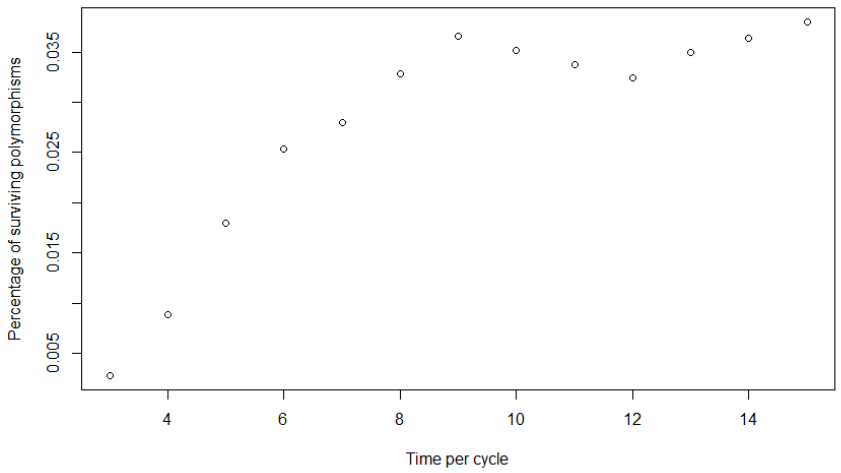

Figure A.1: To ensure the derived criteria are useful I produced parameters at random and then checked whether predicted maintenance matched with simulations. Capacity was set to 100, r_a and r_b were chosen from a uniform distribution between 0.5 and 1.5, while s_a and s_b were taken from the range between 0 and 1. This was done 5000 times per cycle length and time per cycle increased from 3 to 15.

In general these can be fulfilled. I conducted a search for surviving polymorphisms , which could be found, see figure A.1.

A.3 Consecutive Ricker models

Allele A and B compete in the following way: Their frequencies increase according to one Ricker model with capacity $1/f$ and growth rates $r_{s,A}$ and $r_{s,B}$ for t_s generations. The resulting frequencies are normalized and then increase according to another Ricker model with the same capacity and growth rates $r_{w,A}$ and $r_{w,B}$ until generation t_w. They are then normalized to complete the cycle.
During the first phase the frequencies of A during generation t are denoted as $x_{s,t}$, those of B as $y_{s,t}$. During the second phase the frequencies are referred to as $x_{w,t}$ and $y_{w,t}$, where the generations in this phase again start counting from 0.
To understand invasion by the rare type B we again look at the ratio of frequencies after a full cycle and want to see:

$$\frac{y_{w,t_w}}{x_{w,t_w}} > \frac{y_{s,0}}{x_{s,0}} \tag{A.17}$$

Using the same induction as in the Ricker model with winter twice we gain:

$$\begin{aligned} \frac{y_{w,t_w}}{x_{w,t_w}} &= \frac{y_{s,t_s}}{x_{s,t_s}} * e^{(r_{w,B}-r_{w,B})(t_w - f*\sum_{k=0}^{t_w-1}(x_{w,k}+y_{w,k}))} = \\ = \frac{y_{s,0}}{x_{s,0}} * e^{(r_{s,B}-r_{s,A})(t_s - f*\sum_{k=0}^{t_s-1}(x_{s,k}+y_{s,k}))} * e^{(r_{w,B}-r_{w,A})(t_w - f*\sum_{k=0}^{t_w-1}(x_{w,k}+y_{w,k}))} \\ \approx \frac{y_{s,0}}{x_{s,0}} * e^{(r_{s,B}-r_{s,A})(t_s - f*\sum_{k=0}^{t_s-1} x_{s,k})} * e^{(r_{w,B}-r_{w,A})(t_w - f*\sum_{k=0}^{t_w-1} x_{w,k}))} \end{aligned} \tag{A.18}$$

Where the last approximation is justified with B being the rare type. By using

$$\begin{aligned} \frac{1}{r_{w,A}} ln(\frac{x_{w,t_w}}{x_{w,0}}) &= t_w - f\sum_{k=0}^{t_w-1} x_{w,k} \\ \frac{1}{r_{s,A}} ln(\frac{x_{s,t_s}}{x_{s,0}}) &= t_s - f\sum_{k=0}^{t_s-1} x_{s,k} \end{aligned}$$

we can further simplify:

$$\frac{y_{w,t_w}}{x_{w,t_w}} = \frac{y_{s,0}}{x_{s,0}} * (\frac{x_{w,t_w}}{x_{w,0}})^{(\frac{r_{w,B}}{r_{w,A}}-1)} * (\frac{x_{s,t_s}}{x_{s,0}})^{(\frac{r_{s,B}}{r_{s,A}}-1)} \tag{A.19}$$

Plugging this into (A.18) yields:

$$1 < (\frac{x_{w,t_w}}{x_{w,0}})^{(\frac{r_{w,B}}{r_{w,A}}-1)} * (\frac{x_{s,t_s}}{x_{s,0}})^{(\frac{r_{s,B}}{r_{s,A}}-1)} \tag{A.20}$$

Assuming that capacity is approximately reached in each phase (e.g. if t_w and t_s are large), this criterion can be approximated by

$$1 < (\frac{1}{f})^{(\frac{r_{w,B}}{r_{w,A}}-1)} * (\frac{1}{f})^{(\frac{r_{s,B}}{r_{s,A}}-1)} \tag{A.21}$$

which is equivalent to

$$r_{s,B} * r_{w,A} + r_{w,B} * r_{s,A} > 2 * r_{s,A} * r_{w,A} \tag{A.22}$$

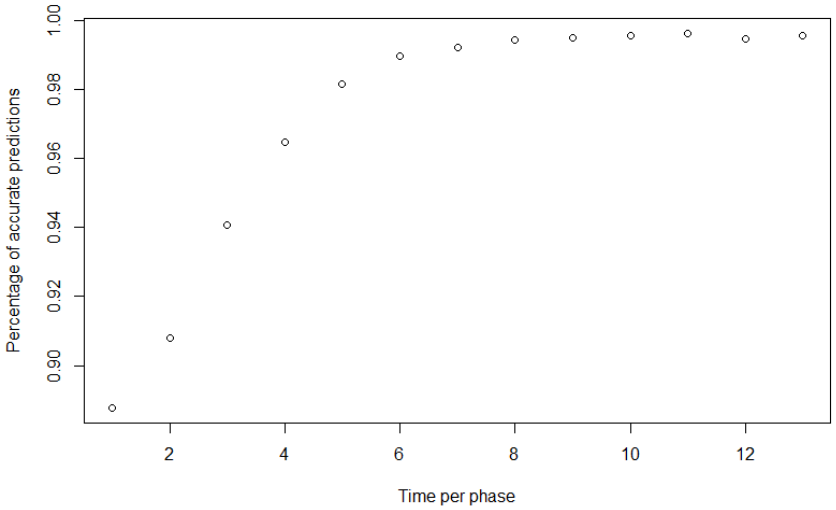

Figure A.2: To ensure the derived criteria are useful I produced parameters at random and then checked whether predicted maintenance matched with simulations. Capacity was set to 100, growth parameters were chosen from a uniform distribution between 0.5 and 1.5. This was done 10 000 times per cycle length and time per cycle increased from 3 to 15.

Similarly allele A can invade if

$$r_{s,B} * r_{w,A} + r_{w,B} * r_{s,A} > 2 * r_{s,B} * r_{w,B} \tag{A.23}$$

To test whether these criteria are useful I did a simulation experiment, where for increasing lengths of the phases growth parameters were drawn from a uniform distribution (so far not parameters with very large fluctuations around the capacity due to runtime issues). Then based on these parameters, theoretical predictions were compared with whether one allele went extinct in the simulation (i.e frequency 10^{-6}) or there was coexistence in a simulation (i.e. frequencies did not change more than $10^{(-12)}$ after a complete cycle or there no extinction happened after 10 000 cycles). This was repeated 10 000 times for each length of phases.

This resulted in accurate predictions, see figure A.2.

A.4 Consecutive Ricker whose capacities differ by a constant factor

Allele A and B compete in the following way: First their frequencies $x_{t,s}$ and $y_{t,s}$ increase for t_s generations according to the recursions:

$$\begin{aligned} x_{t+1,s} &= x_{t,s} * e^{r_{A,s}(1-(x_{t,s}+y_{t,s})/K_{A,s})} \\ y_{t+1,s} &= y_{t,s} * e^{r_{B,s}(1-(x_{t,s}+y_{t,s})/K_{B,s})} \end{aligned} \tag{A.24}$$

Here $K_{A,s}$ and $K_{B,s}$ are the respective summer capacities, and $r_{A,s}$ and $r_{B,s}$ are the respective summer growth rates. In winter then the populations decrease for t_w generations according to

$$\begin{aligned} x_{t+1,w} &= x_{t,w} * e^{r_{A,w}(1-(x_{t,w}+y_{t,w})/K_{A,w})} \\ y_{t+1,w} &= y_{t,w} * e^{r_{B,w}(1-(x_{t,w}+y_{t,w})/K_{B,w})} \end{aligned} \tag{A.25}$$

Here $K_{A,w}$ and $K_{B,w}$ are the respective winter capacities, and $r_{A,w}$ and $r_{B,w}$ are the respective winter growth rates. Further we let

$$\begin{aligned} \frac{K_{A,w}}{K_{B,w}} &= \frac{K_{A,s}}{K_{B,s}} = c \\ \frac{K_{A,w}}{K_{A,s}} &= \frac{K_{B,w}}{K_{B,s}} = f \end{aligned} \tag{A.26}$$

Now assume B to be rare and A to be common. Then to increase in frequency over a year we need:

$$\begin{aligned}
\frac{y_0}{x_0} < \frac{y_{t_w,w}}{x_{t_w,w}} = \frac{y_{t_s,s}}{x_{t_s,s}} * e^{r_{B,w}*(t_w - \frac{1}{K_{B,w}}\sum_{t=0}^{t_w-1}(x_{t,w}+y_{t,w})) - r_{A,w}*(t_w - \frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}+y_{t,w}))} \approx \\
\frac{y_{t_s,s}}{x_{t_s,s}} * e^{r_{B,w}*(t_w - \frac{1}{K_{B,w}}\sum_{t=0}^{t_w-1}(x_{t,w})) - r_{A,w}*(t_w - \frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))} = \\
\frac{y_{t_s,s}}{x_{t_s,s}} * e^{(1-c)*r_{B,w}*t_w + c*r_{B,w}*(t_w - \frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))} * e^{-r_{A,w}*(t_w - \frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))} = \\
\frac{y_{t_s,s}}{x_{t_s,s}} * e^{(1-c)*r_{B,w}*t_w + (c*\frac{r_{B,w}}{r_{A,w}}-1)*ln(\frac{x_{t_w,w}}{x_{t_s,s}})} = \\
\frac{y_0}{x_0} * e^{(1-c)*r_{B,w}*t_w + (c*\frac{r_{B,w}}{r_{A,w}}-1)*ln(\frac{x_{t_w,w}}{x_{t_s,s}})} * e^{(1-c)*r_{B,s}*t_s + (c*\frac{r_{B,s}}{r_{A,s}}-1)*ln(\frac{x_{t_s,s}}{x_{0,s}})}
\end{aligned} \tag{A.27}$$

By taking the logarithm and assuming that capacities are reached in each phase this reduces to:

$$0 < (1-c)(r_{B,w} * t_w + r_{B,s} * t_s) + c * ln(\frac{1}{f})(\frac{r_{B,s}}{r_{A,s}} - \frac{r_{B,w}}{r_{A,w}}) \tag{A.28}$$

Analogously the criterion for invasion of an A allele is:

$$0 < (c-1)(r_{A,w} * t_w + r_{A,s} * t_s) + ln(\frac{1}{f})(\frac{r_{A,s}}{r_{B,s}} - \frac{r_{A,w}}{r_{B,w}}) \tag{A.29}$$

A.5 Summer allele has summer growth advantage, Winter allele winter capacity advantage

Let the frequencies of allele A and allele B be $x_{t,s}$ and $y_{t,s}$ in summer as well as $x_{t,w}$ and $y_{t,w}$ in winter. In summer they reproduce according to Ricker with rates $r_{A,s}$ and $r_{B,s}$ to the common summer capacity K_s. In winter they reproduce according to Ricker, though this time they have respective capacities $K_{A,w}$ and $K_{B,w}$ and share the rate r_w. As before the seasons last for t_s and t_w respectively.

Now assume B to be rare and A to be common. Then to increase in frequency over a year we need:

$$
\begin{aligned}
\frac{y_0}{x_0} < \frac{y_{t_w,w}}{x_{t_w,w}} = \frac{y_{t_s,s}}{x_{t_s,s}} * e^{r_w*(t_w-\frac{1}{K_{B,w}}\sum_{t=0}^{t_w-1}(x_{t,w}+y_{t,w}))-r_w*(t_w-\frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}+y_{t,w}))} \approx \\
\frac{y_{t_s,s}}{x_{t_s,s}} * e^{r_w*(t_w-\frac{1}{K_{B,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))-r_w*(t_w-\frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))} = \\
\frac{y_{t_s,s}}{x_{t_s,s}} * e^{(1-\frac{K_{A,w}}{K_{B,w}})*r_w*t_w+\frac{K_{A,w}}{K_{B,w}}*r_w*(t_w-\frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))} * e^{-r_w*(t_w-\frac{1}{K_{A,w}}\sum_{t=0}^{t_w-1}(x_{t,w}))} = \\
\frac{y_{t_s,s}}{x_{t_s,s}} * e^{(1-\frac{K_{A,w}}{K_{B,w}})*r_w*t_w+(\frac{K_{A,w}}{K_{B,w}}-1)*ln(\frac{x_{t_w,w}}{x_{t_s,s}})} = \\
\frac{y_0}{x_0} * e^{(1-\frac{K_{A,w}}{K_{B,w}})*r_w*t_w+(\frac{K_{A,w}}{K_{B,w}}-1)*ln(\frac{x_{t_w,w}}{x_{t_s,s}})} * e^{(r_{B,s}-r_{A,s})*(t_s-\frac{1}{K_s}\sum_{k=0}^{t_s}(x_{k,s}+y_{k,w}))} \approx \\
\frac{y_0}{x_0} * e^{(1-\frac{K_{A,w}}{K_{B,w}})*r_w*t_w+(\frac{K_{A,w}}{K_{B,w}}-1)*ln(\frac{x_{t_w,w}}{x_{t_s,s}})} * e^{(r_{B,s}-r_{A,s})*(t_s-\frac{1}{K_s}\sum_{k=0}^{t_s}x_{k,s})} = \\
\frac{y_0}{x_0} * e^{(1-\frac{K_{A,w}}{K_{B,w}})*r_w*t_w+(\frac{K_{A,w}}{K_{B,w}}-1)*ln(\frac{x_{t_w,w}}{x_{t_s,s}})} * e^{(r_{B,s}-r_{A,s})*(\frac{1}{r_{A,s}}\log(\frac{x_{t_s,s}}{x_{t_w,w}}))} = \\
\frac{y_0}{x_0} * e^{(1-\frac{K_{A,w}}{K_{B,w}})*r_w*t_w} * (\frac{x_{t_w,w}}{x_{t_s,s}})^{(\frac{K_{A,w}}{K_{B,w}}-\frac{r_{B,s}}{r_{A,s}})}
\end{aligned}
\tag{A.30}
$$

Taking the logarithm and assuming capacities are approximately reached this becomes:

$$
0 < (1-\frac{K_{A,w}}{K_{B,w}})r_w t_w + \log(\frac{K_s}{K_{A,w}})(\frac{r_{B,s}}{r_{A,s}}-\frac{K_{A,w}}{K_{B,w}}) \tag{A.31}
$$

and the analogous criterion for invading A becomes

$$
0 < (1-\frac{K_{B,w}}{K_{A,w}})r_w t_w + \log(\frac{K_s}{K_{B,w}})(\frac{r_{A,s}}{r_{B,s}}-\frac{K_{B,w}}{K_{A,w}}) \tag{A.32}
$$

These can be fulfilled simultaneously.

B Appendix

In this section I cover additional material regarding the establishment probabilities.

B.1 Fixation in periodic models

We will follow the notation of Uecker and Hermisson (2011) [UH11].Allele B tries to invade against common A.

The probability of fixation for a single mutant with selective advantage $s(t)$ is [UH11]

$$p_{fix} = \frac{2}{1 + \int_0^\infty (N(0)/N_e(t)) \exp(-\int_0^t s(\tau)d\tau)dt} \tag{B.1}$$

Here $N_e(t)$ is the variance effective population size given by

$$N_e(t) = \frac{N(t)}{(2\xi(t) + b(t) + d(t) + s(t))} \tag{B.2}$$

$\xi(t) + b(t)$ is the per capita birth rate of the common allele, $\xi(t) + d(t)$ is the per capita death rate.

Let us now assume that $N_e(t+n) = N_e(t)$ and $s(t+n) = s(t)$.

Assume now the initial mutation takes place at time t_0. So we have

$$\begin{aligned}\int_{t_0}^{\infty}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt = \\ \int_{t_0}^{n}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt+ \\ \sum_{j=1}^{\infty}\int_{j*n}^{(j+1)n}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt\end{aligned} \tag{B.3}$$

To simplify this expression we take a look at the terms of the series:

$$\begin{aligned}\int_{j*n}^{(j+1)n}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt = \\ \int_{j*n}^{(j+1)n}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{n}s(\tau)d\tau-\int_{n}^{jn}s(\tau)d\tau-\int_{jn}^{t}s(\tau)d\tau)dt = \\ \exp(-(j-1)\int_{0}^{n}s(\tau)d\tau)\exp(-\int_{t_0}^{n}s(\tau)d\tau)\int_{j*n}^{(j+1)n}(N(t_0)/N_e(t))\exp(-\int_{jn}^{t}s(\tau)d\tau)dt = \\ \exp(-(j-1)\int_{0}^{n}s(\tau)d\tau)\exp(-\int_{t_0}^{n}s(\tau)d\tau)\int_{0}^{n}(N(t_0)/N_e(t))\exp(-\int_{0}^{t}s(\tau)d\tau)dt\end{aligned} \tag{B.4}$$

where we used the fact that $N_e(t+n) = N_e(t)$ and $s(t) = s(t+n)$. We observe that this expression is only dependent on the index j as an exponent of $\exp(-\int_0^n s(\tau)d\tau)$, so we see that (B.3) becomes

$$\begin{aligned}\int_{t_0}^{\infty}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt = \\ \int_{t_0}^{n}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt+ \\ \exp(-\int_{t_0}^{n}s(\tau)d\tau)\int_{0}^{n}(N(t_0)/N_e(t))\exp(-\int_{0}^{t}s(\tau)d\tau)dt \\ *\sum_{j=0}^{\infty}(\exp(-\int_{0}^{n}s(\tau)d\tau))^j\end{aligned} \tag{B.5}$$

The infinite series has now been reduced to a geometric series, where the only assumption we needed so far were that $N_e(t)$ and $s(t)$ are periodic. The criterion for this sum to converge is that $\int_0^n s(\tau)d\tau > 0$, i.e. that the invading allele has a mean advantage over the period. This lends itself to the interpretation that the fixation probability in a periodic scenario is not zero, exactly if the invading allele has a mean advantage over the period. Using the standard formula for the summation of geometric series we gain:

$$\begin{aligned} \int_{t_0}^{\infty}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt = \\ \int_{t_0}^{n}(N(t_0)/N_e(t))\exp(-\int_{t_0}^{t}s(\tau)d\tau)dt + \\ \frac{\exp(-\int_{t_0}^{n}s(\tau)d\tau)\int_0^n(N(t_0)/N_e(t))\exp(-\int_0^t s(\tau)d\tau)dt}{1-\exp(-\int_0^n s(\tau)d\tau)} = \\ F_1(t_0)+\frac{F_2(t_0)}{1-\exp(-\int_0^n s(\tau)d\tau)} \end{aligned} \tag{B.6}$$

Now putting all together we have

$$P_{fix}(t_0) = \frac{2}{1+F_1(t_0)+\frac{F_2(t_0)}{1-\exp(-\int_0^n s(\tau)d\tau)}} \tag{B.7}$$

B.2 Establishment in a specific exponential model with WF in winter

From here we will apply our specific model.

The specific probability depends on the population size $N(t)$, so we need to specify how the population behaves after the summer capacity is reached. We assume that until the onset of winter at t_s the population remains constant and then it falls exponentially to K_w with parameter r_w. We further assume that the selective advantage is constant during the initial growth $s(t) = s_1$ and then again is constant once capacity is reached, s_2.
We will assume that in each phase the rates are constant and denote them ξ_s, ξ_k, ξ_w, b_s,

b_k, b_w, d_s, d_k and d_w, where s subscript denotes the rate during initial growth, k once at capacity and w during the fall back to winter capacity. Further $2\xi_s + b_s + d_s + s_1$ is denoted as c_s, $2\xi_k + b_k + d_k + s_2$ is denoted as c_k and $2\xi_w + b_w + d_w + s_2$ is denoted as c_w.

We will further simplify our problem by assuming that the probability to become established equals the fixation probability in a model where total growth rates are not frequency dependent but are simply those of the common type. This is justified in situations where the total population size is sufficiently large, since once the allele with an advantage reaches moderate numbers, the probability of it not becoming fixed is negligible and as long as the numbers are low the differing growth rates will only make a very small difference. We have three possible starting positions: $t_0 < t_K$, $t_K < t_0 < t_s$ and $t_0 > t_s$.

We will do the calculation for $t_0 < t_K$, in the other cases it can be done in a similar way. First we want to evaluate $F_1(t_0)$:

$$\begin{aligned}
F_1(t_0) = \int_{t_0}^{n} (N(t_0)/N_e(t)) \exp(-\int_{t_0}^{t} s(\tau)d\tau)dt = \\
\int_{t_0}^{t_k} (N(t_0)/N_e(t)) \exp(-\int_{t_0}^{t} s(\tau)d\tau)dt + \int_{t_K}^{n} (N(t_0)/N_e(t)) \exp(-\int_{t_0}^{t} s(\tau)d\tau)dt = \\
\int_{t_0}^{t_k} c_s \exp(r_{A,s}(t_0 - t) - (t - t_0)s_1)dt + \\
\int_{t_K}^{t_s} c_k e^{r_{A,s}(t_0 - t_k)} \exp(-s_1(t_k - t_0) - s_2(t - t_k))dt + \\
\int_{t_s}^{n} c_w \exp(r_{A,s}(t_0 - t_k) - (t - t_s)r_w - s_1(t_k - t_0) - s_2(t - t_k))dt = \\
\frac{c_s(1 - \exp(-(t_K - t_0)(s_1 + r_{A,s})))}{r_{A,s} + s_1} + \\
\frac{c_k \exp(-(t_K - t_0)(s_1 + r_{A,s}))(1 - \exp((t_k - t_s)s_2))}{s_2} + \\
\frac{c_w \exp(-(t_K - t_0)(s_1 + r_{A,s}) - s_2(t_s - t_k))(1 - \exp(-(s_2 + r_w)(n - t_s)))}{r_w + s_2}
\end{aligned} \tag{B.8}$$

Next we evaluate $F_2(t_0)$:

$$
\begin{aligned}
F_2(t_0) = \exp(-\int_{t_0}^{n} s(\tau)d\tau) \int_0^n (N(t_0)/N_e(t)) \exp(-\int_0^t s(\tau)d\tau)dt = \\
e^{(-s_1(t_k-t_0)-s_2(n-t_k))} \int_0^n (N(t_0)/N_e(t)) \exp(-\int_0^t s(\tau)d\tau)dt = \\
N(t_0)e^{(-s_1(t_k-t_0)-s_2(n-t_k))}(\int_0^{t_k} (1/N_e(t)) \exp(-\int_0^t s(\tau)d\tau)dt \\
+ \int_{t_k}^{t_s} (1/N_e(t)) \exp(-\int_0^t s(\tau)d\tau)dt + \int_{t_s}^{n} (1/N_e(t)) \exp(-\int_0^t s(\tau)d\tau)dt) = \\
N(t_0)e^{(-s_1(t_k-t_0)-s_2(n-t_k))}(\int_0^{t_k} \frac{c_s}{K_w} \exp(-(r_{A,s}+s_1)t)dt \\
+ \int_{t_k}^{t_s} \frac{c_k}{K_s} \exp(-s_1t_k - s_2(t-t_k))dt + \int_{t_s}^{n} \frac{c_w}{K_s} \exp(-r_w(t-t_s) - s_1t_k - s_2(t-t_k))dt) = \\
N(t_0)e^{(-s_1(t_k-t_0)-s_2(n-t_k))}(\frac{c_s(1-e^{-(r_{A,s}+s_1)t_k})}{K_w(r_{A,s}+s_1)} + \frac{c_k e^{-s_1t_k}(1-e^{-s_2(t_s-t_k)})}{K_s s_2} \\
+ \frac{c_w e^{-s_1t_k}(e^{-s_2(t_s-t_k)} - e^{-r_w(n-t_s)-s_2(n-t_k)})}{K_s(r_w+s_2)})
\end{aligned}
\tag{B.9}
$$

B.3 Application of modified 16a

Uecker and Hermisson treated the special case where population is constant and selection varies as [UH11]:

$$
s(t) = s_0 + (s_{max} - s_0)\cos(\omega t + \phi) \tag{B.10}
$$

We will derive an approximate solution for the special case where $\phi = 0$ and $s_0$is small. We take $t_0 = n = 2\pi/\omega$. Then the only difficulty lies in calculating G_2.

$$
\begin{aligned}
G_2 = \int_0^{2\pi/\omega} (2\xi + s(t)) \exp(-\int_0^t s(\tau)d\tau)dt = \\
\int_0^{2\pi/\omega} 2\xi \exp(-\int_0^t s(\tau)d\tau)dt - \exp(-\int_0^t s(\tau)d\tau)\Big|_0^{2\frac{\pi}{\omega}} = \\
2\xi \int_0^{2\pi/\omega} \exp(-s_0 t - \frac{(s_{max} - s_0)}{\omega} sin(\omega t)dt + (1 - \exp(-2\frac{2\pi}{\omega})) = \\
= 2\xi \sum_{n=0}^{\infty} \int_0^{2\pi/\omega} \exp(-s_0 t) \frac{(\frac{(s_{max}-s_0)}{\omega} sin(\omega t))^n}{n!} dt + (1 - \exp(-2\frac{2\pi}{\omega}))
\end{aligned}
\tag{B.11}
$$

Here we have used the Taylor expansion of the exponential function.
Define $F_n := \int_0^{2\pi/\omega} sin(\omega t)^n * e^{-s_0 t} dt$. Then straightforwardly $F_0 = \frac{\omega}{s_0}(1 - exp(-\frac{2\pi}{\omega}))$ and by repeated partial integration $F_1 = \frac{1-\exp(-\frac{2\pi}{\omega})}{1+\frac{\omega^2}{s_0^2}}$. For $n > 1$ we have

$$
\begin{aligned}
F_n = \int_0^{2\pi/\omega} sin(\omega t)^n * e^{-s_0 t} dt = \int_0^{2\pi/\omega} sin(\omega t)^{n-2}(1 - \cos(\omega t)^2) * e^{-s_0 t} dt = \\
F_{n-2} - \int_0^{2\pi/\omega} sin(\omega t)^{n-2} \cos(\omega t)^2 * e^{-s_0 t} dt
\end{aligned}
\tag{B.12}
$$

Here we use partial integration

$$
\begin{aligned}
F_n = F_{n-2} - \int_0^{2\pi/\omega} sin(\omega t)^{n-2} \cos(\omega t)^2 * e^{-s_0 t} dt = \\
F_{n-2} - (\frac{\sin(\omega t)^{n-1}}{\omega(n-1)} \exp(-s_0 t) \cos(\omega t)\Big|_0^{2\frac{\pi}{\omega}} + \int_0^{2\pi/\omega} \frac{\sin(\omega t)^{n-1}}{\omega(n-1)} \cos(\omega t) s_0 e^{-s_0 t} dt \\
+ \int_0^{2\pi/\omega} \frac{\sin(\omega t)^n}{(n-1)} e^{-s_0 t} dt) = \\
F_{n-2} - \frac{1}{n-1} F_n - \int_0^{2\pi/\omega} \frac{\sin(\omega t)^{n-1}}{\omega(n-1)} \cos(\omega t) s_0 e^{-s_0 t} dt = \\
F_{n-2} - \frac{1}{n-1} F_n - (\frac{\sin(\omega t)^n}{\omega^2(n-1)n} \exp(-s_0 t)\Big|_0^{2\frac{\pi}{\omega}} - \int_0^{2\pi/\omega} \frac{\sin(\omega t)^n}{\omega^2 n(n-1)} s_0^2 e^{-s_0 t} dt) = \\
F_{n-2} - \frac{1}{n-1} F_n - \frac{s_0^2}{\omega^2(n-1)n} F_n
\end{aligned}
\tag{B.13}
$$

This gives us the recursion:

$$F_n = \frac{n(n-1)}{n^2 + \frac{s_0^2}{\omega^2}} F_{n-2} \approx \frac{n(n-1)}{n^2} F_{n-2} \tag{B.14}$$

So we can approximate $F_{2m} = \frac{(2m)!}{((2m)!!)^2} F_0$ and $F_{2m+1} = \frac{(2m+1)!}{((2m+1)!!)^2} F_1$. With this (B.11) becomes:

$$\begin{aligned}
G_2 - (1 - \exp(-2\frac{2\pi}{\omega})) = 2\xi \sum_{n=0}^{\infty} \int_0^{2\pi/\omega} \exp(-s_0 t) \frac{(\frac{(s_{max}-s_0)}{\omega} sin(\omega t))^n}{n!} dt = \\
2\xi (\sum_{n=0}^{\infty} \int_0^{2\pi/\omega} e^{-s_0 t} \frac{(\frac{(s_{max}-s_0)}{\omega} sin(\omega t))^{2n}}{(2n)!} dt + \sum_{n=0}^{\infty} \int_0^{2\pi/\omega} e^{-s_0 t} \frac{(\frac{(s_{max}-s_0)}{\omega} sin(\omega t))^{2n+1}}{(2n+1)!} dt) = \\
2\xi (\sum_{n=0}^{\infty} \frac{(\frac{(s_{max}-s_0)}{\omega})^{2n} F_{2n}}{(2n)!} + \sum_{n=0}^{\infty} \frac{(\frac{(s_{max}-s_0)}{\omega})^{2n+1} F_{2n+1}}{(2n+1)!}) \approx \\
2\xi (F_0 \sum_{n=0}^{\infty} \frac{(\frac{(s_{max}-s_0)}{\omega})^{2n}}{((2n)!!)^2} + F_1 \sum_{n=0}^{\infty} \frac{(\frac{(s_{max}-s_0)}{\omega})^{2n+1}}{((2n+1)!!)^2}) = \\
2\xi (F_0 I_0(\frac{(s_{max}-s_0)}{\omega}) + F_1 \frac{\pi}{2} L_0(\frac{(s_{max}-s_0)}{\omega}))
\end{aligned} \tag{B.15}$$

Here I_0 is a modified Bessel function of the first kind and L_0 is a modified Struve function.

Plugging into the expression for P_{fix} we get:

$$\begin{aligned}
P_{fix} \approx \frac{2}{1 + \frac{G_2}{1 - \exp(-s_0 \frac{2\pi}{\omega})}} = \frac{1}{1 + \frac{\xi (F_0 I_0(\frac{(s_{max}-s_0)}{\omega}) + F_1 \frac{\pi}{2} L_0(\frac{(s_{max}-s_0)}{\omega}))}{1 - \exp(-s_0 \frac{2\pi}{\omega})}} \\
= \frac{1}{1 + \frac{s_0}{\omega} \xi I_0(\frac{(s_{max}-s_0)}{\omega}) + \frac{\pi \xi}{2(1 + \frac{\omega^2}{s_0^2})} L_0(\frac{(s_{max}-s_0)}{\omega}))}
\end{aligned} \tag{B.16}$$

C Appendix

C.1 Source code

```
1  //creates matrices with establishment or survival probabilities as .txt files
2
3  #include "stdafx.h"
4  #include <iostream>
5  #include <boost\random.hpp>
6  #include <math.h>
7  #include <fstream>
8  #include <boost/random/random_device.hpp>
9
10 boost::random_device dev;
11 boost::mt19937 rng( dev );
12
13 typedef float reals;
14
15 typedef long int naturals;
16
17
18 // going through a year cycle:
19 void yearcycle(naturals & population_A, naturals& population_B, naturals K_summer,
20 naturals t_s, naturals t_w, naturals t_0, float s1, float s2, float r_w, float r1, float r2)
21 {
22
23
24 naturals t = t_0;
25
26 while ((population_A + population_B < K_summer) && (t < t_s) && ((population_A >0) && (population_B >0)))
27 {
28
29
30 if (((population_A >0) && (population_B >0)))
31 {
32 boost::poisson_distribution<> offspringdist_A(exp(r1)*population_A);
33 boost::variate_generator<boost::mt19937&, boost::poisson_distribution<> > children_A(rng, offspringdist_A);
34 population_A = children_A();
35
36 boost::poisson_distribution<> offspringdist_B(exp(r2)*population_B);
37 boost::variate_generator<boost::mt19937&, boost::poisson_distribution<> > children_B(rng, offspringdist_B);
38 population_B = children_B();
39 }
40
41 t++;
42
43
44
45 }
46
47
48
49 for (naturals  j = t; j < t_s; j++)
50 {
51
```

```
52  boost::binomial_distribution<> coindist_s(K_summer, (1 + s2)*population_B / ((1 + s2)*population_B + population_A));
53  boost::variate_generator<boost::mt19937&, boost::binomial_distribution<> > unfaircoin(rng, coindist_s);
54
55  int offspring = unfaircoin();
56
57
58
59  population_B = offspring;
60  population_A = K_summer - offspring;
61
62
63  }
64
65  int capacity = K_summer;
66
67  for (naturals j = t_s; j <= t_s + t_w; j++)
68  {
69
70
71  boost::binomial_distribution<> coindist_s(capacity, (1 + s2)*population_B / ((1 + s2)*population_B + population_A));
72  boost::variate_generator<boost::mt19937&, boost::binomial_distribution<> > unfaircoin(rng, coindist_s);
73
74  naturals offspring = unfaircoin();
75
76
77
78  population_B = offspring;
79  population_A = capacity - offspring;
80
81  capacity = exp(r_w)* capacity;
82
83
84  }
85
86
87  }
88
89
90  int main()
91  {
92
93
94
95
96  // capacities
97  naturals K_summer = 10000;
98  naturals  K_winter = 10000;
99
100
101 //length of seasons
102 naturals  t_s = 10;
103 naturals  t_w = 5;
104
105 //starting time during year
106 naturals  t_0=0;
107
108
109 // winter growthrate ensures return to winter capacity during winter
110
111 reals  r_w = -log((float) K_summer / K_winter) / t_w;
112
113
114
115 //number of years
116 naturals iterationdepth = 100 ;
117
118
119 boost::poisson_distribution<> coindist(5);
120 boost::variate_generator<boost::mt19937&, boost::poisson_distribution<> > faircoin(rng, coindist);
121
122 reals establishment_A[100][100] = { 0 };
```

```
123 reals establishment_B[100][100] = { 0 };//calculated probabilities
124 reals mutual_establishment[100][100] = { 0 };
125 reals longterm_survival[100][100] = { 0 };
126
127 naturals selectioncoefs = 70;
128 naturals growthcoeffs = 70;
129
130
131
132 naturals t = t_0;
133 naturals n=0;
134
135
136
137
138 std::cout << "Varying growth rates press 1, selection size difference press 2";
139
140 naturals choice;
141
142 std::cin >> choice;
143
144
145 ////// mode 1 //////
146 reals  s = 0.01;
147 if (choice == 1)
148 {
149 for (naturals l = 0; l < selectioncoefs; ++l) //selection strength increases
150 {
151
152 reals s1 = s;
153 reals s2 = s;
154 s *= std::pow(100, (double)1 / selectioncoefs);
155 reals r2 = 0.1;
156 for (naturals k = 0; k < growthcoeffs; ++k) //absolute malthusean parameters from 0.5 to 2
157
158 {
159
160 reals r1 = r2 + s1;
161
162
163 // checking for establishment probabilities of the summer allele
164
165 for (naturals i = 0; i < 100; i++)
166 {
167 // starting populations for establishment of B
168 naturals population_A = K_winter;
169 naturals population_B = 1;
170
171 if (t_0 >0)
172 yearcycle(population_A, population_B, K_summer, t_s, t_w, t_0, s1, s2, r_w, r1, r2);
173
174 for (naturals year = 0; (population_B < 0.3 *K_winter) && (population_B>0) &&
175  (population_A > 0) && (year < iterationdepth); year++)
176 {
177 yearcycle(population_A, population_B, K_summer, t_s, t_w, 0, s1, s2, r_w, r1, r2);
178
179 }
180
181
182
183
184 establishment_B[l][k] += (int)(population_B > 0);
185 bool B_survival = (population_B > 0);
186
187 // starting populations for establishment of A
188 population_A = 1;
189 population_B = K_winter;
190
191 if (t_0 >0)
192 yearcycle(population_A, population_B, K_summer, t_s, t_w, t_0, s1, s2, r_w, r1, r2);
193
```

```
194 for (naturals year = 0; (population_A < 0.3 *K_winter) && (population_A>0) &&
195  (population_B > 0) && (year < iterationdepth); year++)
196 {
197
198
199 yearcycle(population_A, population_B, K_summer, t_s, t_w, 0, s1, s2, r_w, r1, r2);
200
201 }
202
203 establishment_A[l][k] += (naturals)(population_A > 0);
204
205 mutual_establishment[l][k] += (naturals)(B_survival*population_A > 0);
206
207 }
208
209 r2 += 1.5 / growthcoeffs;
210 }
211
212 }
213 }
214 std::cout << std::endl << std::endl;
215
216
217
218 /////// mode 2//////////////
219
220
221
222
223 if (choice == 2)
224 {
225
226
227 reals r2 = log(2);
228 K_winter = 10000;
229 K_summer = 1000000;
230 r_w = -log((float)K_summer / K_winter) / t_w;
231 iterationdepth = 300;
232
233 reals s2 = 0.01;
234
235 for (naturals l = 0; l <= selectioncoefs; ++l) //selection strength increases
236 {
237
238 reals s1 = 0.01;
239
240 for (naturals k = 0; k <= growthcoeffs; ++k) //absolute malthusean parameters from 0.5 to 2
241
242 {
243
244 reals r1 = r2 + s1;
245
246
247 // checking for establishment probabilities of the summer allele
248
249 for (int i = 0; i < 100; i++)
250 {
251 // starting populations
252 naturals population_A = K_winter;
253 naturals population_B = 1;
254
255
256
257 for (naturals year = 0; (population_B < 0.3 *K_winter) && (population_B>0) &&
258  (population_A > 0) && (year < iterationdepth); year++)
259 {
260
261
262 yearcycle(population_A, population_B, K_summer, t_s, t_w, 0, s1, s2, r_w, r1, r2);
263
264 }
```

```
265
266 establishment_B[l][k] += (int)(population_B > 0);
267
268 bool B_survival = (population_B > 0);
269
270
271 population_A = 1;
272 population_B = K_winter;
273
274
275
276 for (naturals year = 0; (population_A < 0.3 *K_winter) && (population_A >0) &&
277  (population_B > 0) && (year < iterationdepth); year++)
278 {
279
280
281 yearcycle(population_A, population_B, K_summer, t_s, t_w, 0, s1, s2, r_w, r1, r2);
282
283 }
284
285 establishment_A[l][k] += (int)(population_A > 0);
286
287 mutual_establishment[l][k] += (int)(B_survival*population_A > 0);
288
289 population_A = K_winter / 2;
290 population_B = K_winter / 2;
291
292
293
294 for (naturals year = 0; (population_A>0) && (population_B > 0) && (year < iterationdepth); year++)
295 {
296
297
298 yearcycle(population_A, population_B, K_summer, t_s, t_w, 0, s1, s2, r_w, r1, r2);
299
300
301
302 }
303 longterm_survival[l][k] += (int)((population_A >0) && (population_B >0));
304
305
306 }
307 s1 *= std::pow(100, (double)1 / growthcoeffs);
308
309
310
311 }
312 s2 *= std::pow(100, (double)1 / selectioncoefs);
313 std::cout << s1 <<" " << s2 << std::endl;
314 }
315
316 }
317
318
319
320 //printing stuff into .txt files
321
322
323 std::ofstream myfile_B;
324 myfile_B.open("establishment_B.txt");
325 for (int l = 0; l < selectioncoefs; ++l)
326 {
327 for (int k = 0; k < growthcoeffs ; ++k)
328 {
329 myfile_B << establishment_B[l][k] << " ";
330 }
331 myfile_B << std::endl;
332 }
333 myfile_B.close();
334
335 std::ofstream myfile_A;
```

```
336 myfile_A.open("establishment_A.txt");
337 for (int l = 0; l < selectioncoefs; ++l)
338 {
339 for (int k = 0; k < growthcoeffs; ++k)
340 {
341 myfile_A << establishment_A[l][k] << " ";
342 }
343 myfile_A << std::endl;
344 }
345 myfile_A.close();
346
347
348 std::ofstream myfile_M;
349 myfile_M.open("establishment_M.txt");
350 for (int l = 0; l < selectioncoefs; ++l)
351 {
352 for (int k = 0; k < growthcoeffs; ++k)
353 {
354 myfile_M << mutual_establishment[l][k] << " ";
355 }
356 myfile_M << std::endl;
357 }
358 myfile_M.close();
359
360
361 std::ofstream myfile_sur;
362 myfile_sur.open("survival.txt");
363 for (int l = 0; l <= selectioncoefs; ++l)
364 {
365 std::cout << l;
366 for (int k = 0; k <= growthcoeffs; ++k)
367 {
368 myfile_sur << longterm_survival[l][k] << " ";
369 }
370 myfile_sur << std::endl;
371 }
372 myfile_sur.close();
373
374 std::cin >> K_summer;
375
376
377 //printing in window
378
379
380 for (int l = 0; l < selectioncoefs; ++l)
381 {
382 for (int k = 0; k < growthcoeffs; ++k)
383 {
384 std::cout << establishment_B[l][k] << " ";
385 }
386 std::cout << std::endl;
387 }
388
389 std::cout << std::endl;
390 std::cout << std::endl;
391
392 for (int l = 0; l < selectioncoefs; ++l)
393 {
394 for (int k = 0; k < growthcoeffs; ++k)
395 {
396 std::cout << establishment_A[l][k] << " ";
397 }
398 std::cout << std::endl;
399 }
400 std::cout << std::endl;
401 std::cout << std::endl;
402
403
404
405 for (int l = 0; l < selectioncoefs; ++l)
406 {
```

```
407 for (int k = 0; k < growthcoeffs; ++k)
408 {
409 std::cout << mutual_establishment[l][k] << " ";
410 }
411 std::cout << std::endl;
412 }
413 std::cout << std::endl;
414 std::cout << std::endl;
415
416
417
418 for (int l = 0; l < selectioncoefs; ++l)
419 {
420 for (int k = 0; k < growthcoeffs; ++k)
421 {
422 std::cout << longterm_survival[l][k] << " ";
423 }
424 std::cout << std::endl;
425 }
426
427 std::cin >> K_summer;
428 return 0;
429 }
```

D Abstract

Eine der wesentlichen Fragen der mathematischen Populationsgenetik ist der Erhalt genetischer Diversität. Alle Lebewesen sind zeitlichen Fluktuationen ausgesetzt. Frühe Ergebnisse in der Populationsgenetik legten nahe, dass haploide Diversität durch zeitliche Fluktuation nicht erhalten wird, da sich jeweils das Allel mit der größten geometrisch mittleren Fitness durchsetzt. Im Kontrast dazu haben neuere theoretische Studien Mechanismen identifiziert, die durchaus mithilfe von zeitabhängiger Selektion Polymorphismen erhalten können. Diese beruhen darauf, dass sobald eine gegebene Dichte erreicht wird, die Umgebung sich ändert. Somit werden häufige Allele benachteiligt, da Umgebungen in denen sie höhere Wachstumsraten haben nur für eine kurze Zeit bestehen. Allerdings waren diese Modelle nicht auf ökologisch relevante Szenarien angepasst. In dieser Arbeit werden mehrere ökologisch relevante Modelle eingeführt, die Allele in einer Spezies mit hoher Generationenzahl über einen Jahresverlauf beschreiben. Für das Überleben von Polymorphismen wurden nach Möglichkeit exakte Kriterien, oder sonst robuste Näherungskriterien hergeleitet. Um das Verhalten dieser Mechanismen auch in stochastischen Kontext zu verstehen wurden Simulationsexperimente durchgeführt so wie Methoden aus der Populationsgenetik auf diesen Kontext angepasst um Invasionswahrscheinlichkeiten zu berechnen.

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