Thesis for the degree of Master of Science in Engineering Physics

Dynamics of sex ratio and genetics in populations with mixed sexual and asexual reproduction

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Abstract

Biological populations that reproduce both sexually and asexually are frequent in nature. An example is the brown algae *Fucus radicans* that is endemic to the Baltic Sea and reproduces both sexually and through cloning. This species displays intriguing patterns of sex ratio and genetic diversity. A specific female genotype, sometimes referred to as the *superfemale* [I], is widespread and dominates in large regions [1]. Perhaps surprisingly, comprehensive experiments where plants have been cultivated in vitro show no sign of the superfemale having a higher fitness than other genotypes [2]. How a joint effect of sexual and asexual reproduction affects this species is not fully explored, and the research could benefit from a better understanding of the consequences of this reproductive strategy.

Within this master's thesis, two models for a population with mixed sexual and asexual reproduction and neutral genetics have been developed and explored. One model describes a well-mixed population, and the other a spatially structured one. Based on the results obtained for these models, we argue that populations with both reproduction types have a tendency to adopt a certain sex ratio. We find that geographic structure favors asexual reproduction and enables one genotype without selective advantages to colonize empty habitat through cloning. This mechanism provides a *clonal wave* that could explain the dominating female observed in *F. radicans*. In the long run and if sexual reproduction is high enough, this dominant clone will be replaced by a pattern of mixed genotypes as a second *sexual wave* establishes sexual reproduction. Fluctuations counteract the effect of the sexual wave and may cause the population to consist of local *clonal islands* of only one sex, surrounded by regions where sexual reproduction persists. We explore the question whether the mechanisms provided in the models can explain the patterns observed in *F. radicans* populations.

Acknowledgements

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Contents

1 | Introduction

Biological populations that reproduce both sexually and asexually are frequent in nature. Examples include widespread species such as common trees, lichens and ferns [ii]. The bonnethead shark is an example of an animal that has both types of reproduction [3]. *Fucus radicans* is a dieoecious[1] brown algae that is endemic to the Baltic Sea and whose reproduction is both sexual and through cloning. It was first described in 2005, and it is in the focus of active research within marine biology [4]. The species seems to have originated recently through local adaption to the Baltic Sea, and its ability to reproduce clonally is an important example of such an adaption. A more comprehensive introduction of *F. radicans* is given in Section 1.1.

The consequences of the reproductive strategies of this species are not fully explored, and a better understanding of the joint effect of sexual and asexual reproduction could contribute to the knowledge of this species. A mathematical model can provide insight into the complex dynamics of biological populations, especially if mathematical calculus is combined with computer simulations [5].

In this Master's Thesis two models that have been designed to explore the dynamics of populations with mixed sexual and asexual reproduction are analyzed. Analytical results are presented, as well as results from computer simulations. Many variants of reproduction, sexes, and inheritance are found in nature, but a model has to build upon specific assumptions. Therefore the populations modeled are assigned similar properties as real populations of *F. radicans*.

The population dynamics and population genetics in populations that reproduce both sexually and asexually are different from in those populations that have only one of the reproduction types. If a dieoecious population is fully sexual, then both sexes must persist for the population to be able to survive, whereas asexual reproduction allows for persistence with one sex only. Sexual reproduction can enable a migrant that arrives to a population consisting only of the opposite sex to establish sexual reproduction where previously reproduction was purely asexual. We will show that such a pop-

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[1]That is: The species has distinct female and male organisms.

ulation can be driven towards a certain sex ratio. This sex ratio depends sensitively upon the conditions for reproduction; the amount of female and male cloning, and upon the amount of sexual reproduction. Different conditions imply qualitatively different fates of the population.

Under some conditions, a population is driven towards a stable sex ratio with both females and males. Demographic fluctuations counteract this tendency and cause a sex ratio that varies over both space and time. Eventually, in a finite population, fluctuations must lead to loss of a sex and loss of sexual reproduction. This will happen more frequently in small populations, than in large populations.

Populations of *F. radicans*, as well as others, are geographically structured. This implies that reproduction and competition to some extent is local. When competing for space individuals can be out-competed even though there is empty habitat somewhere else. An individual can only mate within a local part of the population and, even if both sexes are present globally, they have to be present locally for sexual reproduction. We will show how asexual reproduction in this way is favored by locality.

Fluctuations of the sex ratio are large for small local populations, and a sex is lost frequently. Such a loss can imply that, locally, reproduction is purely asexual. If both sexes exists globally there is however a chance that the lost sex will eventually spread and re-establish sexual reproduction. We will show how fluctuations provide a mechanism that lead to that a population consists of local "islands" of clones of only one sex, surrounded by regions with both sexes where sexual reproduction persists. Fluctuations and spreading cause these *clonal islands* to drift; they grow, shrink and move over time.

Spatial structure affects the pattern of genetic variation. When a sex can be locally absent this has even further implications on the population genetics. Locally the diversity will be reduced, since no new genotypes are formed from sexual reproduction. We will see that the clonal islands will be compositions of relatively few genotypes that can persist for a long time.

When reproduction is local, colonization of empty habitat will originate from populated regions. The colonization is facilitated by asexual reproduction in that no mating partner is required. This mechanism can allow one clone to colonize all the empty habitat as a *clonal wave* that sweeps over it. After such a clone has invaded, sexual reproduction can also invade since the clone that colonized is a potential mating partner. This gives the possibility for a second, sexual, wave to arise that replaces the total domination of the original clone. The *sexual wave* brings a situation where individuals of both sexes are present and reproduction is both sexual and asexual.

In the recent years, plants of *F. radicans* have been samples at several times and locations, and samples have been analyzed genotypically and

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phenotypically. The data show that the species displays a spatially varying pattern of sex ratio and genetic diversity.

We will show how the variation in sex ratio can be explained by how the population dynamics depends on local conditions affecting the effectiveness of cloning and sexual reproduction. The colonization of empty habitat and the approach of a stable steady state is explored, and is important for understanding this species since it is young and could be in a transient phase. We will show that variation over space and time of the sex ratio can be explained by fluctuations that may cause drifting clonal islands.

Some local populations of *F. radicans* are dominated by one or a few clones, whereas others are more diverse. A specific female genotype is widespread. She occurs in more than half of the species' geographical area and dominates in large regions. She is sometimes referred to as the *superfemale* [I]. Comprehensive in vitro experiments provide no support for that the superfemale genotype has a higher fitness than other genotypes [2]. An explanation for the superfemale, that does not assume her to have inherited advantages, is therefore of high interest. We will demonstrate that a mechanism for the superfemale to dominate, despite being selectively neutral, can be found in the clonal wave caused by locality of reproduction during colonization. If the expansion of *F. radicans* went in the form of a clonal wave consisting of the superfemale, she will be dominating by being first at place.

Complicating this hypothesis is that, despite dominating, the superfemale has neighbors with other genotypes; for some populations a mosaic of different clonal lineages are reported. Explanations for the interruptions of the superfemale might be found in that the sexual wave brings variation when sweeping over her. Fluctuations allow for a mosaic of genotypes containing both the superfemale and other clones. As will be discussed, it is however not obvious that a superfemale without selective advantages will stay dominant after the sexual wave has passed.

1.1 *Fucus radicans*

Fucus radicans is a brown algae that reproduces both sexually and through cloning. It is endemic to the Baltic Sea, where it lives at 2 - 8 meters depth. The taxon was first described as a species in 2005, and it is descending from the brown algae *Fucus vesiculosus*[2] whose plants are larger, and with which it shares most of its habitat [4]. The geographical distribution of *F. radicans* and *F. vesiculosus* can be seen in Figure 1.1.

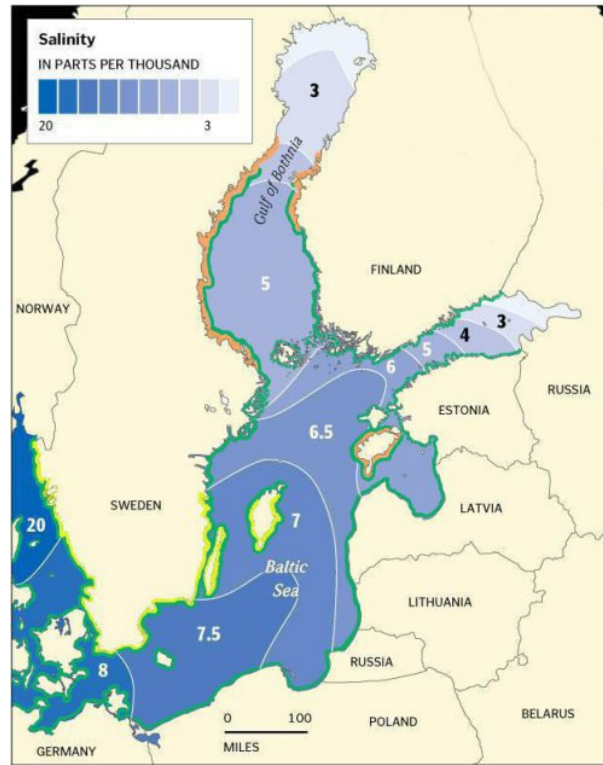[2]Commonly called "bladder wrack" in English and "blåstång" in Swedish.

*Figure 1.1: Distribution of **Fucus**-species and salinity in the Baltic Sea. **F. radicans** occurs along coasts marked with orange color, **F. vesiculosus** occurs along coasts marked with green color. Yellow color indicates a third **Fucus**-species, **Fucus serratus**, but for this species, only distribution along Swedish coasts is shown. Reproduced from [6], with permission.*

F. radicans was argued to be a separate species because it was thought to be reproductively isolated from *F. vesiculosus* [4]. But a later study has shown that hybridization between the two species may be possible [7]. Here, one concluded that the two species can hybridize, but the fertility of the hybrids were not investigated. Furthermore, no observations of hybrids are reported for in vivo populations [8].

The Baltic sea is a particular marine environment in that the water is brackish. It is also a young sea in that it came to exist after the most recent glacial period. Since then, the sea has gone through different geological transitions, until reaching its current form around 7500 to 4000 years ago. The current form is a brackish sea, with a salinity gradient that declines from around 8 ‰ (mass, surface water) at the straits of Öresund to around 2 ‰ in the northern and eastern distal parts (see Figure 1.1). The salinity is low when compared with the surface waters in oceans where the salinity is on average 35 ‰.

Since the Baltic Sea is a relatively young sea, the speciation that gave rise to *F. radicans* must have, on timescales of evolution, happened recently and proceeded fast. Actually, calculations based on data from nine micro-satellites in *F. radicans* and *F. vesiculosus* have indicated that the divergence started sometime between 125 and 2475 years ago. The posterior probability peaks for the divergence to have happened around 400 years ago [9].

While *F. vesiculosus* is widespread over the northern hemisphere, *F. radicans* was formed inside the Baltic Sea [9]. The ability of *F. radicans* to reproduce clonally is considered as an important adaption to low salinity, since it is expected that sexual reproduction is less effective for *Fucus*-species in low-salinity waters. Both *F. radicans* and *F. vesiculosus* display both sexual and asexual reproduction, but whereas clonal reproduction in *F. vesiculosus* is reported as an exception, *F. radicans* is considered to be mainly clonal, at least in some locations [1].

Individuals are, in both species, either females or males. Both female and male plants reproduce clonally by releasing *adventitious branches*. These branches grow near the stem of the plant and are released into the water where they sink and are able to attach to the ground and grow into adult plants. The number of adventitious branches that each plant of *F. radicans* releases was examined in vitro, and the results show no sign of that one of the sexes is more prone to cloning than the other [I]. Sexual reproduction is performed through releasing of sperms and eggs into the water [I]. Eggs are fertilized in the water and zygotes sink to the ground and are able to grow into new plants [I].

Examinations of the spatial patterns of sex ratio of *F. radicans* have shown local populations consisting mostly of females. Also, genetic analysis have shown intriguing spatial patterns that are illustrated in Figure 1.2. A specific female genotype is to be found along all the Swedish and some of the Finnish coasts where *F. radicans* lives [1]. This genotype is numerous and widespread and is therefore described as *dominating* and referred to as the *superfemale* [I]. The superfemale coexists with other genotypes, of which some are large local clones.
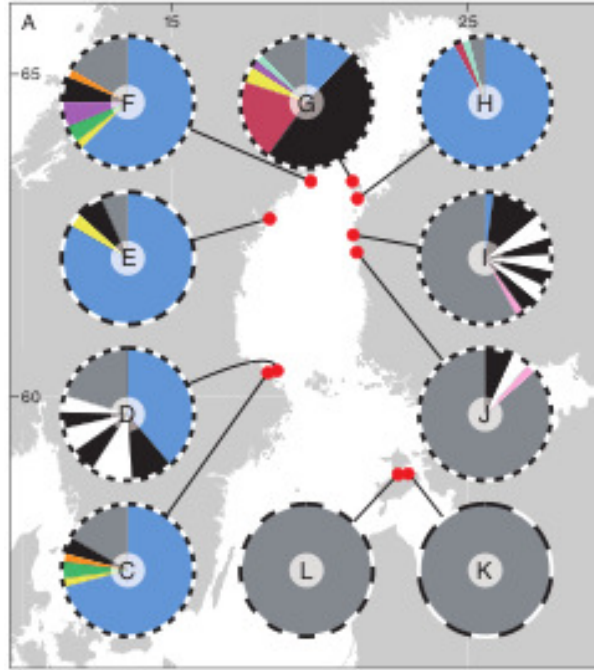
*Figure 1.2: Genotypes observed for **F. radicans** at different sites. Gray segments show the proportion of unique genotypes at a site. Black and white segments show genotypes found in two or more copies, but unique to the particular site. Colored segments show genotypes observed in more than one site. The number of plants that were analyzed are indicated by black and white frames. Reproduced from [1], with permission.*

Plants of three different genotypes, of which one belonged to the super-female, have been cultivated in vitro to asses differences in fitness. nine different fitness parameters were investigated. The results of this study shows no sign of that the superfemale genotype has a higher fitness than other genotypes [2].

Since *F. radicans* was described, it has been in the focus of active research within marine biology where different topics are investigated. One important task lies in explaining the spatial patterns of sex ratio and genotypes that are observed.

2 | Method

To asses the properties of populations with mixed sexual and asexual reproduction two models were designed and implemented. One is a well-mixed model, and the other a spatially explicit model. The artificial biology in both models aims to resemble the biology of *F. radicans*. They are both designed under the same assumptions, and therefore the spatially explicit model describes how a population in the well-mixed model would be affected by geographical structure. The dynamics of the well-mixed model allows for mathematical analysis, and the precise results obtained for the well-mixed model are used for understanding of the more complex dynamics of the spatially explicit model.

2.1 The well-mixed model

The model describes a dieoecious well-mixed population with mixed sexual and asexual reproduction. The amount of sexual vs. asexual reproduction depends on the sex ratio in the population. It is assumed that genetics are neutral in that, except for the sex of an individual, no attributes affecting the properties of an individual are inherited. In the following, a precise description of the population dynamics of the model is presented, and after that follows an interpretation of it.

2.1.1 Description of the well-mixed model

- Discrete and non-overlapping generations.

- The population consists of N individuals.

- The number of females in generation τ is denoted $N_{f,\tau}$ and the number of males is denoted $N_{m,\tau}$. Individuals are either females or males; $N_{f,\tau} + N_{m,\tau} = N$.

- An individual in generation $\tau + 1$ is assigned according to these probabilites

    - a clonally recruited female:

$$p_{c_f,\tau+1} = \frac{c_f N_{f,\tau}}{c_f N_{f,\tau} + c_m N_{m,\tau} + s\frac{N_{f,\tau} N_{m,\tau}}{N}}$$

    - a clonally recruited male:

$$p_{c_m,\tau+1} = \frac{c_m N_{m,\tau}}{c_f N_{f,\tau} + c_m N_{m,\tau} + s\frac{N_{f,\tau} N_{m,\tau}}{N}}$$

    - sexually recruited:

$$p_{s,\tau+1} = \frac{s\frac{N_{f,\tau} N_{m,\tau}}{N}}{c_f N_{f,\tau} + c_m N_{m,\tau} + s\frac{N_{f,\tau} N_{m,\tau}}{N}},$$

    where s, c_f and c_m are constants, the *sexual birth rate* and the female and male *clonal birth rates*, respectively. A sexually produced individual is assigned to be a female or a male with equal probabilities.

2.1.2 Interpretation

The clonal growth rates, c_f and c_m, determine the number of adventitious branches (see Section 1.1) produced by an individual in each generation. Each female produces c_f adventitious branches and each male produces c_m adventitious branches. Therefore $c_f N_{f,\tau}$ female and $c_m N_{m,\tau}$ male clonal branches are produced in generation τ.

The number of zygotes produced in generation τ equals $s\frac{N_{f,\tau} N_{m,\tau}}{N}$. This number is proportional to the number of female-male pairs, $N_{f,\tau} N_{m,\tau}$, a correlation that can be expected if the probability of fertilization for a gamete (an egg or a sperm) is low. When this probability is low, the number of eggs and sperms that have not been "consumed" during the time fertilization occurs remains approximately constant. If most eggs and sperms are never involved in a fertilization, it can be derived from collision theory that the number of zygotes produced is proportional to both $N_{f,\tau}$ and $N_{m,\tau}$. The

number of zygotes produced is *frequency dependent*; it is proportional to the number of females times the frequency of males, or the number of males times the frequency of females [1].

Zygotes and clonal branches produced in generation τ compete for entering generation $\tau + 1$ as adult plants. The genetics are neutral in that all offspring have the same chance of success. Thus, the competition is a sampling of N offspring, and the outcome depends only on the number of competing agents. If, for instance, the number of female clones that compete is twice the number if male clones that compete, then the probability to sample a female clone is twice the probability to sample a male clone.

The sexual growth rate, s, gives the effectiveness of sexual reproduction in that s: 1) Contains the chance of collision between one sperm and one egg (i. e. fertilization) and 2) Adjusts for that the probability of a zygote to form an adult plant is likely to be different from the probability of an adventitious branch to form an adult plant.

From the above, we have that the number of individuals in generation τ that are sampled from is given by

$$c_f N_{f,\tau} + c_m N_{m,\tau} + s \frac{N_{f,\tau} N_{m,\tau}}{N}.$$

We assume that the number of competing individuals is large compared with N, the number of adult individuals, and thus the probabilities for sampling a clonal female, a clonal male and a sexual recruit are determined by the formulae given.

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[1]The alternative to frequency dependence is *density dependence*. If the number of zygotes was density dependent, it would be given by $sN_{f,\tau}N_{m,\tau}$.

2.2 The spatially explicit model

The model describes how a population as in the well-mixed model is affected by geographical structure. As for the well-mixed model, the algorithm is presented first, and after that follows an interpretation of it.

2.2.1 Description of the spatially explicit model

- Discrete and non-overlapping generations.

- Population is distributed over M cells in a one-dimensional[2] array with periodic boundary conditions.

- Each cell contains between 0 and K individuals. Each individual is either a female or a male.

- In one generation each individual disperses adventitious branches in its vicinity. A female disperses c_f female adventitious branches and a male disperses c_m male adventitious branches. An adventitious branch inherits the genotype of its (asexual) parent.

- In one generation each male disperses s sperms in its vicinity.

- A sperm that was dispersed to cell i lands on a female with the probability $N_{f,i}/K$, where $N_{f,i}$ is the number of females in cell i. If the sperm landed on a female a zygote is produced, and it is dispersed around the female. The zygote is assigned to be a female or a male with equal probabilities, and it is assigned a unique genotype.

- All dispersals (sperms, zygotes and adventitious branches) have a random and Gaussian range, whose standard deviation is σ; an element in cell i is dispersed to a cell j, where

$$j = \text{int}(X), \quad X \sim \mathcal{N}(i, \sigma^2). \tag{2.1}$$

- Zygotes and adventitious branches are the offspring, and they candidate to become adult individuals in the next generation. If the number of offspring that were dispersed to a cell is $> K$, then K offspring are sampled to form adult individuals in that cell. If the number of offspring is $\leq K$, all offspring become adult individuals.

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[2]The model can be implemented in more dimensions than one.

2.2.2 Interpretation

As is shown in Appendix A, this spatially explicit model is similar to the previously described well-mixed model. It is explained how the well-mixed model is approached as the dispersal range grow, and each cell approaches the dynamics of the well-mixed model as the dispersal range is reduced. Therefore, the spatially explicit model illustrates how a population in the well-mixed model is affected by geographical structure.

The important difference is that reproduction and competition is local in the spatially explicit model. Only groups of individuals within a region with a size of order of σ can communicate - that is: reproduce sexually and have offspring that compete.

The number of sperms a that male produces in the model is regulated by the parameter s. One such "artificial sperm" corresponds in to a large number of real sperms in real populations, a number of sperms that, if they are in the close vicinity of a female are roughly expected to cause one fertilization. With "roughly expected" we imply that s may also adjust for that zygotes and adventitious branches might not have the same chance of survival. This is analogous the adjusting function of s in the well-mixed model (see Section 2.1.2), and thus s gives the effectiveness of sexual reproduction also in the spatially explicit model.

For a sperm to fertilize, an egg is needed. Therefore the probability for the sperm to fertilize in a cell equals the density of females in that cell. The dispersal of adventitious branches is straightforward; it is as in the well-mixed model, but with geographical structure added.

A dispersal range drawn from a Gaussian distribution implies that the dispersed elements are spread in the vicinity of the origin. The probability for dispersals of exceptionally long range is negligible. The dispersal range of eggs is small compared to the dispersal range of sperms in *F. radicans* [I]. Therefore, we assume no egg dispersal and that the fertilization takes place at the location of the female. The dispersal range of zygotes and adventitious branches are of the same order in *F. radicans* [I]. We therefore assume that they can be regulated with the same parameter, σ.

One could pose the question whether one parameter is enough for regulating all dispersals. Would it not be reasonable to introduce a parameter σ_s for sperms and let σ_s be larger than σ? Such an extension of the model was only superficially explored, and is discussed in Chapter 4.

K is the carrying capacity of a cell. This carrying capacity mirrors the size of a region that a such cell in reality would correspond to. Here, a competition of space takes place, since at most K adult individuals can live in a region of that size. The genetics are neutral in that the competition is

a neutral sampling from the competitors.

There is a strong connection between the parameters K and σ, since the number of individuals that can communicate scales as σK. A small K and a large σ and a large K and small σ can give communicating groups with equally many individuals.

The genetics in this model approximates the genetics of biological populations. In biological populations, a sexually produced offspring has, through recombination at meiosis, a genotype that is sampled from a huge set of possible genotypes. On the contrary, the genotype of a clonal progeny can only differ from the genotype of its (asexual) parent through point mutations, and the differences between these are therefore small. This motivates why a sexually produced individual is assigned a unique genotype, and a clonal offspring inherits the genotype of its (asexual) parent.

3 | Results

This chapter describes the results obtained from the models. The first part is for the well-mixed model, and the second part is for the spatially explicit model. The relative simplicity of the well-mixed model allows for quantitative analysis. This is used later to understand the more complex dynamics of the spatially explicit model. The results for the spatially explicit model allow us to formulate qualitative mechanisms for the dynamics of the sex ratio and the genetics. These results are described with text rather than equations. Results regarding the sex ratio are presented for both models, while results regarding genetics are only presented for the spatially explicit model.

Since the sex ratio is frequently discussed in this chapter, we introduce the notation for it here. To describe the sex ratio we use x_f to denote the frequency of females. We therefore have the frequency of males given by $1 - x_f$ and the ratio females/males given by $x_f/(1 - x_f)$. To describe the frequency of females in generation τ we add τ as a subscript; $x_{f,\tau}$.

3.1 The well-mixed model

For the well-mixed model, results are presented for the dynamics of the sex ratio - that is: how the number of males and females change over time and how this change depends on the parameters. Quantitative results are presented, and for derivations of these we refer either to appendices or to published articles. Section 3.1.6 contains plots that illustrate the dynamics.

3.1.1 Updating of the sex ratio

It follows from the design of the model that the frequency of females in generation $\tau + 1$ is drawn from a binomial distribution;

$$x_{f,\tau+1} \sim \frac{1}{N}\text{Bin}(N, p_{f,\tau+1}). \tag{3.1}$$

Here, $p_{f,\tau+1}$ is the probability that an individual is assigned to be female in generation $\tau + 1$. The stochastic updating of the sex ratio can be seen

in Figures 3.1 and 3.2 in Section 3.1.6. In Appendix B it is concluded that $p_{f,\tau+1}$ is given by

$$p_{f,\tau+1} = \frac{c_f x_{f,\tau} + \frac{1}{2} s x_{f,\tau}(1 - x_{f,\tau})}{c_f x_{f,\tau} + c_m(1 - x_{f,\tau}) + s x_f(1 - x_{f,\tau})}. \tag{3.2}$$

3.1.2 Independent parameters

Adding to the previous, it is concluded in Appendix B that the dynamics of the model is described by the two independent parameters c_f/s and c_m/s, rather than the actual values of c_f, c_m and s. That is: the conditions for a realization is completely described by the two parameters c_f/s and c_m/s, the population size N and the initial conditions. Equation (3.2) can thus be expressed with c_f/s and c_m/s as

$$p_{f,\tau+1} = \frac{\frac{c_f}{s} x_{f,\tau} + \frac{1}{2} x_{f,\tau}(1 - x_{f,\tau})}{\frac{c_f}{s} x_{f,\tau} + \frac{c_m}{s}(1 - x_{f,\tau}) + x_f(1 - x_{f,\tau})}. \tag{3.3}$$

Thus, in the deterministic limit of $N \to \infty$, the sex ratio will update accoding to

$$x_{f,\tau+1} = \frac{\frac{c_f}{s} x_{f,\tau} + \frac{1}{2} x_{f,\tau}(1 - x_{f,\tau})}{\frac{c_f}{s} x_{f,\tau} + \frac{c_m}{s}(1 - x_{f,\tau}) + x_f(1 - x_{f,\tau})}. \tag{3.4}$$

The average of many realizations follows this recursive formula well, as is shown in Figure 3.3 in Section 3.1.6.

3.1.3 Absorbing states of the sex ratio

$x_f = 1$ and $x_f = 0$ are absorbing states of the sex ratio. This means that, if females are lost they will remain lost in all future generations, and, if males are lost they will remain lost in all future generations. The former can be formulated either as *loss* of females or *fixation* of males, and the latter as loss of males or fixation of females. An example of fixation of females (and loss of males) is found in the left panel of Figure 3.1. In Figure 3.2 loss of females and loss of males are seen in both panels.

3.1.4 Steady states of the sex ratio

In Appendix B, it is concluded that there are three cases for the steady states of the sex ratio, and that these cases are given by the parameters c_f/s and c_m/s:

1. Two steady states if $\frac{c_f}{s} - \frac{c_m}{s} \geq \frac{1}{2}$:

    (a) Fixation of females ($x_f^* = 1$) - stable
    (b) Fixation of males ($x_f^* = 0$) - unstable

2. Three steady states if $\left| \frac{c_f}{s} - \frac{c_m}{s} \right| < \frac{1}{2}$:

    (a) Fixation of females ($x_f^* = 1$) - unstable
    (b) Both sexes present ($x_f^* = \frac{1}{2} + \frac{c_f}{s} - \frac{c_m}{s}$) - stable
    (c) Fixation of males ($x_f^* = 0$) - unstable

3. Two steady states if $\frac{c_m}{s} - \frac{c_f}{s} \geq \frac{1}{2}$:

    (a) Fixation of females ($x_f^* = 1$) - unstable
    (b) Fixation of males ($x_f^* = 0$) - stable

Thus, we have bifurcations in parameter space at $\frac{c_f}{s} - \frac{c_m}{s} = \frac{1}{2}$ and $\frac{c_m}{s} - \frac{c_f}{s} = \frac{1}{2}$. We emphasize that there is one steady state containing both females and males if and only if

$$\left| \frac{c_f}{s} - \frac{c_m}{s} \right| < \frac{1}{2}. \tag{3.5}$$

This steady state is stable and given by

$$x_f^* = \frac{1}{2} + \frac{c_f}{s} - \frac{c_m}{s}. \tag{3.6}$$

The stable steady state in Equation (3.6) will henceforth be referred to as the *non-trivial steady state*. The absorbing states are also steady states and will be referred to as the *trivial steady states*. We notice that sexual reproduction is needed for the non-trivial steady state to exist ($s > 0$). In Figure 3.4 it is shown that, Equation (3.4) predicts a faster approach of the non-trivial steady state when sexual reproduction is increased in relation to asexual.

The tendency for the sex ratio to approach a non-trivial steady state is shown in Figure 3.1. In Figure 3.2 all three cases for the stable steady state are shown.

3.1.5 Effect of fluctuations

If we have a non-trivial stable steady state and both sexes present, the sex ratio tends to approach this steady state. For a finite population size, the stochasticity of the model can however cause loss of one of the sexes; the binomial trials for assigning sexes to individuals allows for "all females" and "all males". As mentioned, these are absorbing states, and if a sex is lost before the non-trivial steady state is reached, the stable steady state will not be reached. On the contrary, in the deterministic limit $N \to \infty$, the non-trivial stable steady state will always be reached from any state where neither females or males are lost.

After a non-trivial steady state is reached, the sex ratio will fluctuate around it if the population size is finite. Deviations from a non-trivial steady state has a tendency to decrease and the non-trivial steady state will likely be reached again. Therefore we will have a sex ratio that wiggles around the non-trivial steady state. This can be seen in Figure 3.1.

Even after the non-trivial steady state is reached the sex ratio can, due to fluctuations, end up in a trivial steady state. This was the case for one of the realizations shown in the left panel of Figure 3.1. Generally, if there is are absorbing states that can be reached for a stochastic system, they must eventually be reached. And, if there is also an attractor for this system, it is known that the average time to reach the absorbing state(s) from the attractor will scale exponentially with the system size if the system size is large [10, 11]. This means that, for the well-mixed model, there is always a non-zero probability for a finite population to loose one of the sexes, and therefore this will eventually happen. And, if we are in a non-trivial steady state, the average time until one of the sexes is lost scales exponentially with the population size if the population size is large. If we denote the average time until one of the sexes is lost $\overline{T}_{\text{loss}}$, we have that

$$\overline{T}_{\text{loss}} \sim C e^{k(c_f/s, c_m/s)N}, \tag{3.7}$$

where k is function of the parameters c_f/s and c_m/s and C is a constant. k, and therefore the average time to loss of one of the sexes, will increase with increasing sexual reproduction (decreasing c_f/s and c_m/s). This is expected from that we know that the sex ratio is driven towards the non-trivial steady state through sexual reproduction. The exponential time to loss of one of the sexes was verified through simulations and is shown in Figure 3.5. The function $k(c_f/s, c_m/s)$ was explored for $c_f = c_m$ and the results are shown in Figure 3.6.

3.1.6 Plots

Figure 3.1 illustrates the dynamics of the sex ratio with non-trivial steady states. We note that the stable steady states are approached, and that fluctuations cause the sex ratio to wiggle around them. It is shown that the effect of fluctuations is reduced with increasing N. In the left panel, an example of absorption is shown; one of the red curves reaches $x_f = 1$, and remains there forever (males where lost).

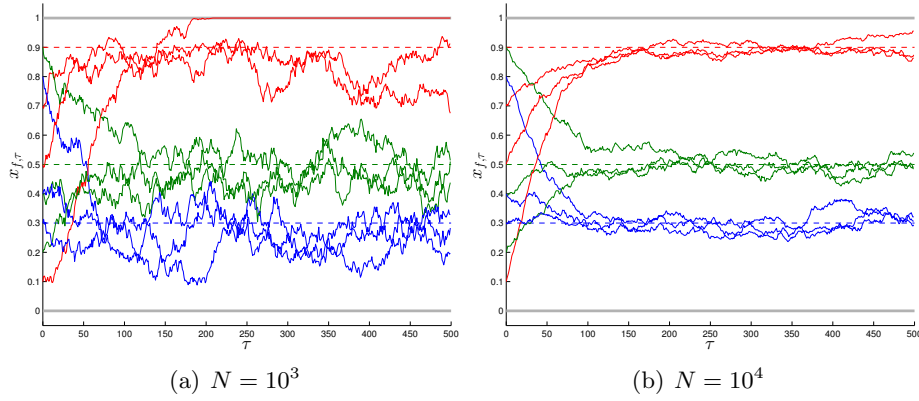(a) $N = 10^3$ (b) $N = 10^4$

Figure 3.1: Dynamics of the sex ratio with a non-trivial steady state. The panels are for different values of N. Solid lines are results from simulations, dashed lines are the steady states, and thick gray lines are the absorbing states. Parameters used: $c_m/s = 10$, Red: $c_f/s = 10.4$, Green: $c_f/s = 10$, Blue: $c_f/s = 9.8$.

In Figure 3.2 the trivial steady states are compared with the non-trivial steady state. The green color is for parameters that imply a non-trivial steady state (equally many males and females in this case), the other colors are for parameters where only trivial steady states exists. The population sizes are as in Figure 3.1, and the effects of fluctuations are smaller in the right panel since N is larger. We note that, when loss/fixation happens, it is not due to fluctuations, but due to that it is the stable steady state.

(a) $N = 10^3$ (b) $N = 10^4$

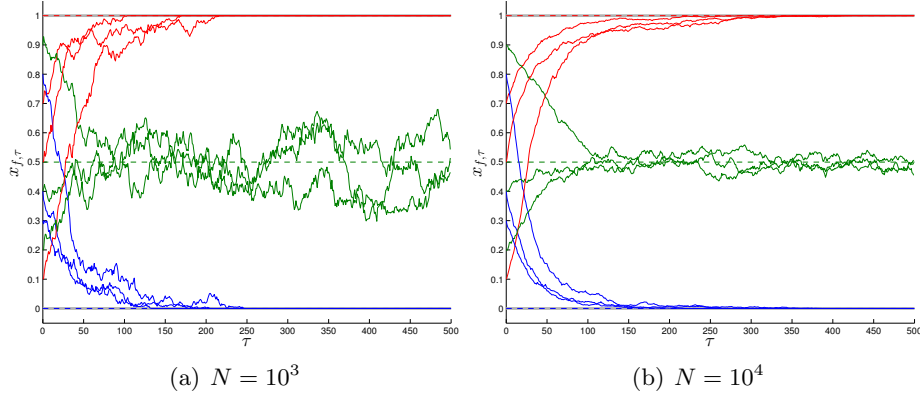Figure 3.2: *Dynamics of the sex ratio with only trivial steady states (red and blue color) and with a non-trivial steady state (green color). The panels are for different values of N. Solid lines are results from simulations, dashed lines are the steady states, and thick gray lines are the absorbing states. Parameters used: $c_m/s = 10$, Red is $c_f/s = 10.6$, Green is $c_f/s = 10$, Blue is $c_f/s = 9.3$.*

Figure 3.3 illustrates the average of 100 simulations for the parameter values used in Figures 3.1 and 3.2. It is shown that despite fluctuations in individual runs, on average, the theoretical prediction of Equation (3.4) is correct. In the top-left plot the average x_f is larger than the theoretical prediction. This is due to that some realizations have reached absorption (compare with the left panel of Figure 3.1).

(a) $N = 10^3$

(b) $N = 10^4$
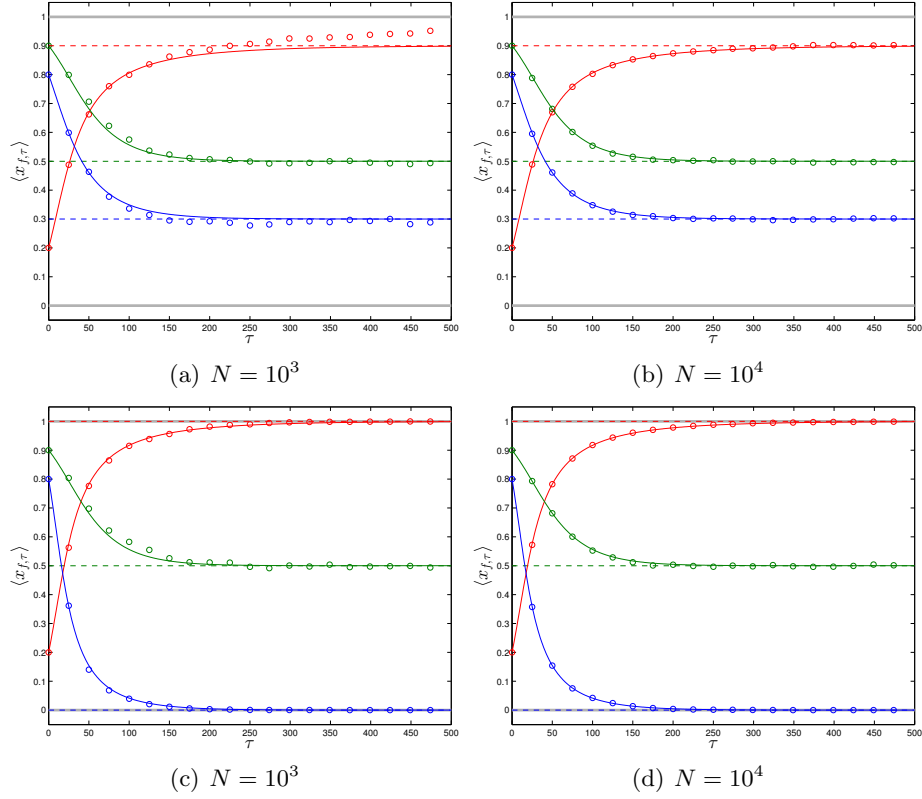
(c) $N = 10^3$

(d) $N = 10^4$

Figure 3.3: *Average $x_{f,\tau}$ as a function of τ for the settings in Figures 3.1 and 3.2. Rings are averages of 100 simulations, thin solid lines are theoretical values, dashed lines are the steady states, and thick gray lines are the absorbing states. Parameters used in top plots: as in Figure 3.1. Parameters used in bottom plots: as in Figure 3.2.*

Figure 3.4 illustrates the impact of the parameters. The colors denote the same stable steady states as in Figure 3.1 (left panel) and Figure 3.2 (right panel). We note that the stable steady state is approached faster when sexual reproduction is large in relation to clonal.
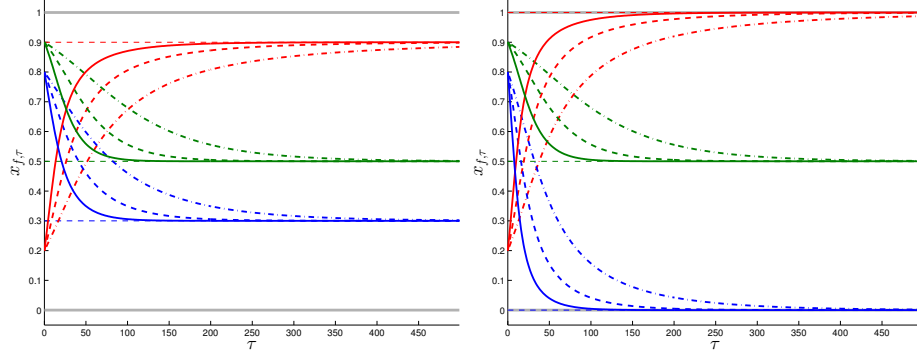

Figure 3.4: $x_{f,\tau}$ as a function of τ for different parameters. Lines are theoretical predictions from Equation (3.4). Solid lines are $c_m/s = 5$, dashed lines are $c_m/s = 10$, dash-dotted lines are $c_m/s = 20$. Left plot: Red is $c_f/s = c_m/s + 0.4$, green is $c_f/s = c_m/s$, and blue is $c_f/s = c_m/s - 0.2$. Right plot: Red is $c_f/s = c_m/s + 0.6$, green is $c_f/s = c_m/s$, and blue is $c_f/s = c_m/s - 0.7$.

Figure 3.5 shows the average time to loss of one of the sexes. Here $c_f = c_m \equiv c$. We note the exponential correlation for large population sizes, and that the time increases with increased sexual reproduction.

(a) $s/c = 20, 10, 5, 2, 1$
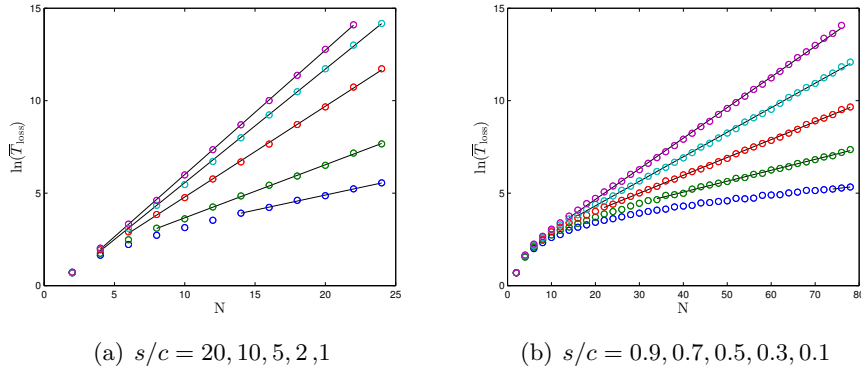
(b) $s/c = 0.9, 0.7, 0.5, 0.3, 0.1$

Figure 3.5: The average time to loss as a function of N for different values of s/c. The times are found by averaging over 1000 simulations. Linear fits have been taken from $N = \lceil \frac{2}{k} \rceil$.

Before loss of a sex, the sex ratio will spend most of its time around its non-trivial steady state. We have introduced

$$p_{s,\max}(s,c) \equiv \frac{s}{s + 4c} \tag{3.8}$$

to denote the probability of sexual origin for an individual in the steady state. Linear fits have been taken to obtain the values of $k(p_{s,\max})$, and in Figure 3.6, the result is shown. Again we notice that the average time to loss increases with the amount of sexual reproduction. In Appendix C it is derived that for a fully sexual population ($p_{s,\max} = 1$), the average time to loss is 2^{N-1} ($k = \ln(2)$). Indeed, in Figure 3.6, it is shown that k approaches $\ln(2)$ as $p_{s,\max}$ approaches 1.
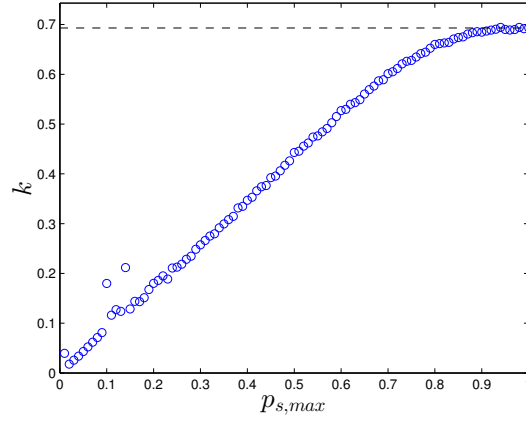

Figure 3.6: *k as a function of $p_{s,max}$. Dashed line is $k = \ln(2)$ for comparison.*

3.2   The spatially explicit model

As mentioned in the introduction to this chapter, the results for the spatially explicit model are mainly qualitative mechanisms for the sex ratio dynamics and the genetics that are described in text. Therefore, the following section consists of text that explains these mechanisms together with plots that illustrate them.

The dynamics of the spatially explicit model is related to the dynamics of the well-mixed model. We explain how we use this knowledge to understand the more complex dynamics in the spatially explicit model. Since the genetic results presented are strongly connected to the dynamics of the sex ratio, the dynamics for the sex ratio is presented before the genetics. After that, the genetics for populations in the spatially explicit model are described. This is done by illustrating the genetics that correspond to realizations already shown for the sex ratio.

Color coding

There are two types of color coding used to present realizations of the spatially explicit model; one to illustrate the sex ratio and one to illustrate the genetics:

- Illustration of sex ratio: color indicates the frequency of females in a cell, with the exception of cells containing only males that are indicated by blue color. Empty cells are gray.

- Illustration of genetics: the color indicates number of unique genotypes in a cell. In this way the plots aim to illustrate the local genetic diversity. Empty cells are gray.

Initializations

For the realizations presented in the following, there are five ways in which the population was initialized. These are presented here, and are referred to in the figures:

- One male, one female:
  One male placed in cell $M/4$ and one female placed in cell $3M/4$. The rest of the habitat is empty.

- Male and female colony:
  The first half of the habitat is filled up with males, and the second half is filled up with females.

- Uniform:
  The habitat is filled up with uniformly distributed males and females.

- Uniform, middle:
  The 100 cells in the middle of the habitat are filled up with uniformly distributed males and females. The rest of the habitat is empty.

- Male-Both-Female:
  The 100 cells in the middle of the habitat are filled up with uniformly distributed males and females. The 100 cells on the left side of this region are filled up with males, the 100 cells on the right side are filled up with females.

3.2.1 Relation to the well-mixed model

In Appendix A we learn how the well-mixed model can be obtained from the spatially explicit model when $\sigma = 0$ and in the limit $\sigma \to \infty$. We can use this knowledge to understand the more complicated dynamics of the spatially explicit model; for a finite and non-zero σ the population consists of local groups of individuals that communicate, and their internal properties will resemble the properties of a well-mixed model. The reducing limits helps us to understand the spatially explicit model, but it is what happens for a finite and non-zero that makes the spatially explicit model interesting; we explore how the well-mixed population can be affected by geographical structure. Therefore we will henceforth assume a finite and non-zero σ, unless something else is stated.

For the well-mixed model, the dynamics were described by the two independent parameters c_f/s and c_m/s, rather than the actual values of c_f, c_m and s. This is approached for the spatially explicit model if we let s, c_f and c_m increase towards infinity and keep the ratios c_f/s and c_m/s constant. However, this approach was not explored and therefore the specific values of c_f, c_m and s were used and will be presented.

3.2.2 Clonal waves

Sexual reproduction demands that a male disperses a sperm to a female. If this communication does not take place, either due to that one of the sexes is absent globally[1] or due to that the sexes are spatially separated, reproduction will be purely clonal. Since clonal offspring can populate an empty cell, we will have expanding clonal colonies[2]. Over time, expansion of a clonal colony is in the form of a wave that washes over empty habitat, and we will therefore call such expansions *clonal waves*. Note that this is not only a diffusive process; the wave has a direction and a preserved shape. Female and male clonal waves are shown in Figure 3.7.

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[1]Absent in the entire habitat.

[2]A clonal colony will expand only if the clonal birth rate, c_f or c_m, are > 1, so that the number of individuals are allowed to grow.
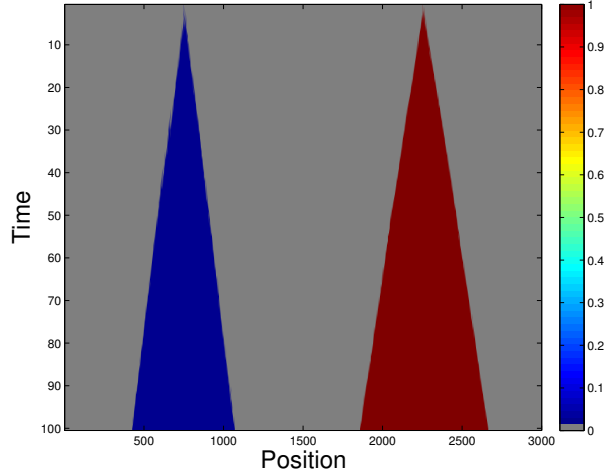
Figure 3.7: Clonal waves causing expansion of clonal colonies. Parameters: $s = 5$, $c_f = 3$, $c_m = 2$, $\sigma = 3$, $K = 10$. The initialization was "One male one female". For color notation and initialization, see the beginning of Section 3.2.

3.2.3 Sexual waves

Sexual reproduction demands communication between males and females; a sperm must be able to disperse to a female. For clonal colonies, if both sexes are present in the population, their clonal colonies must get closer to each other. The spatial separation between females and males is expected to decrease and, within time, sexual reproduction must be allowed. Therefore sexual reproduction must eventually take place if both sexes are present.

We learned the possible cases for the steady state of the sex ratio and their conditions for the well-mixed model. Spatially explicit populations consists of local communicating groups with similar properties as a well-mixed population, and the criterion for a non-trivial steady state locally should therefore resemble the conditions in the well-mixed model (see Equation (3.5)):

$$\left| \frac{c_f}{s} - \frac{c_m}{s} \right| < \frac{1}{2}.$$

Thus, if this criterion is met, we will have local groups where the non-trivial steady state

$$x_f^* = \frac{1}{2} + \frac{c_f}{s} - \frac{c_m}{s},$$

is approached (see Equation (3.6)).

Such groups contain both sexes, and therefore sexual reproduction takes place in the border of a clonal region and a sexual region. Just as clonal

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colonies can invade empty cells, sexual regions can invade a clonal colony; a zygote or an adventitious branch of the opposite sex can be dispersed into it so that sexual reproduction is established. A non-trivial steady state is an attractor that will, with time, be approached locally and spread spatially. Just as the clonal wave, the spatial spreading is also in the form of a wave, and we therefore refer to it as the *sexual wave*. Sexual waves invading clonal colonies are seen in Figure 3.8.
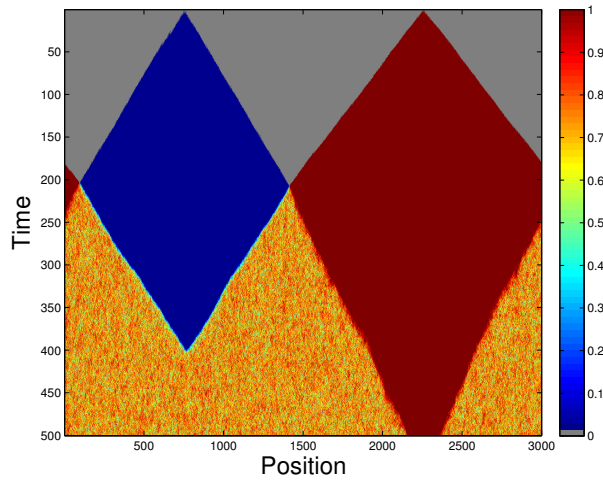
Figure 3.8: Sexual waves invading clonal colonies (continuation of the realization in Figure 3.7). For color notation, see the beginning of Section 3.2.

Even though a non-trivial steady state of the sex ratio exists, the sexual wave can be counteracted by fluctuations. Fluctuations can cause loss of one sex in the sexual wave front, and thereby interrupt its progress. They might even cause previously sexual regions to be replaced by clonal, even though a non-trivial steady state exists. In Figure 3.9 realizations with large and small effects of fluctuations are compared, and both interruption of the sexual wave and clonal regions replacing sexual regions are seen. The effects of fluctuations increase with decreasing σ, K and s. Fluctuations and their effects are further described in Section 3.2.8.

(a) Large effects of fluctuations   (b) Small effects of fluctuations

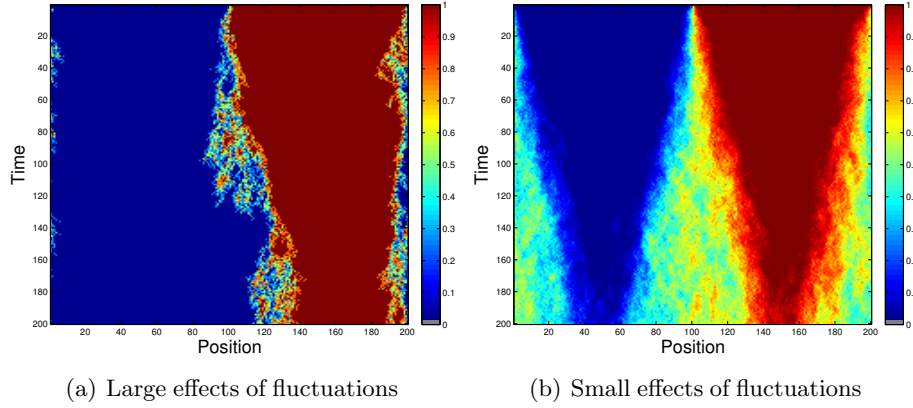*Figure 3.9: Effect of fluctuations on the sexual wave. In the left panel the fluctuations are prominent and effectively hinders the sexual wave, whereas they are smaller in the right panel and the sexual wave is unaffected. In the left panel fluctuations cause previously sexual regions to at a later time become clonal (of only one sex). In the left panel we have $K = 4$ and in the right panel we have $K = 100$. Other parameters are in both panels: $s = 10$, $c_f = 100$, $c_m = 100$, $\sigma = 1$. The initializations were "Male and female colony". For color notation and initialization, see the beginning of Section 3.2.*

3.2.4   Asymmetry between females and males

The well-mixed model was symmetric between sexes when $c_f = c_m$, but not when the clonal birth rates differed. Note that the spatially explicit model is asymmetric even when the female and male clonal birth rates are identical; sperms disperse into female clonal regions and the zygotes produced disperse around their mother. This implies that sexual reproduction takes place more around females than around males. Thus a female is more likely to be replaced by a male than a male is to be replaced by a female. This affects both the speed of the sexual wave and the steady state of the sex ratio. For equal clonal birth rates, $c_f = c_m$, sexual waves move slightly faster into female clonal regions than into male clonal regions, and the steady state is shifted slightly towards containing less females than males. Figure 3.10 demonstrates that, for equal clonal birth rates, the sexual wave moves faster into a female clonal region than into a male clonal region. The shift of the sex ratio is demonstrated in the right panel of Figure 3.17 in Section 3.2.7.
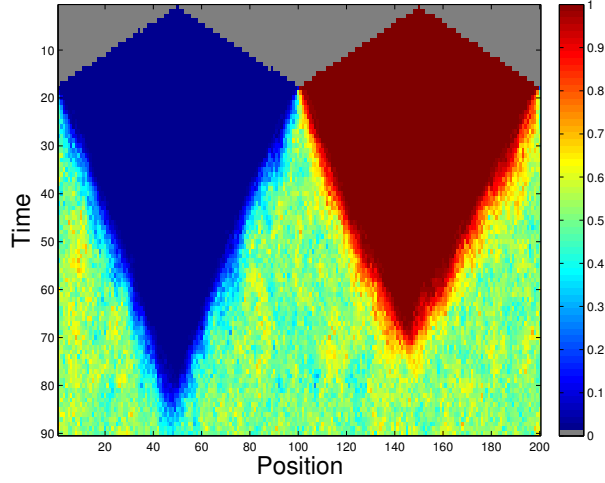
Figure 3.10: Asymmetry between sexes: Sexual waves move faster into female clonal regions than into male clonal regions when the sexes have equal clonal birth rates. Parameters: $s = 100$, $c_f = 100$, $c_m = 100$, $\sigma = 1$, $K = 100$. The initialization was "One male, one female". For color notation and initialization, see the beginning of Section 3.2.

3.2.5 Consequences of wave speeds

The speed of a sexual wave has been found to increase when s and/or σ increase. It decreases with c_f and c_m. Indeed, in Appendix D it is derived that, in specific limits and for equal female and male clonal birth rates ($c_f = c_m = c$), the speed of the sexual wave into clonal regions is given by

$$v_s = \sigma \sqrt{\frac{s}{c}}. \tag{3.9}$$

For some parameter settings, sexual waves move with lower speeds than clonal waves. Then, colonization from a founder colony of both sexes will be by a clonal wave that is followed by a sexual wave. If the sexual wave moves with higher speed than the clonal, the clonal wave will not be seen since the sexual wave always catches it up. Colonization will then go as a sexual wave. In Figure 3.11 two cases are shown; in the left panel the sexual wave does not catch up the female or male clonal wave, in the right panel both clonal waves are caught up.

(a) The sexual waves does not catch up the clonal waves.
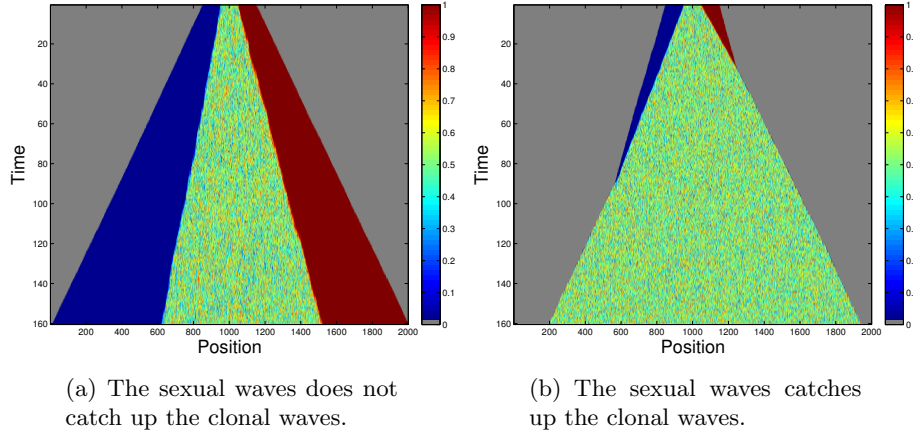
(b) The sexual waves catches up the clonal waves.

Figure 3.11: The speed of the clonal and sexual waves and their implications on colonization. In the left panel the clonal waves move faster than the sexual waves, and colonization goes in the form of one male and one female clonal wave. In the right panel the sexual waves move faster, the clonal waves are caught up and colonization goes in the form of two sexual waves. The clonal birth rates are in the left panel $c_f = c_m = 50$ and in the right panel $c_f = c_m = 4$. Other parameters are in both panels: $s = 200$, $\sigma = 2$, $K = 10$. The initialization was "Male-Both-Female". For color notation and initialization, see the beginning of Section 3.2.

We can conclude that, if there exists a non-trivial steady state, five kinds of clonal and sexual waves may occur:

- Female clonal waves

- Male clonal waves

- Sexual waves into females

- Sexual waves into males

- Sexual waves into empty habitat

The speed of each wave type depends on the parameters. Thus the parameters determine conditions for a specific wave type to colonize empty habitat. For example, we can have parameters allowing for colonization to go as a female clonal wave, but not as a male, and vice versa. These cases are illustrated in Figure 3.12.

(a) The sexual waves catches up the male clonal wave, but not the female.

(b) The sexual waves catches up the female clonal wave, but not the male.
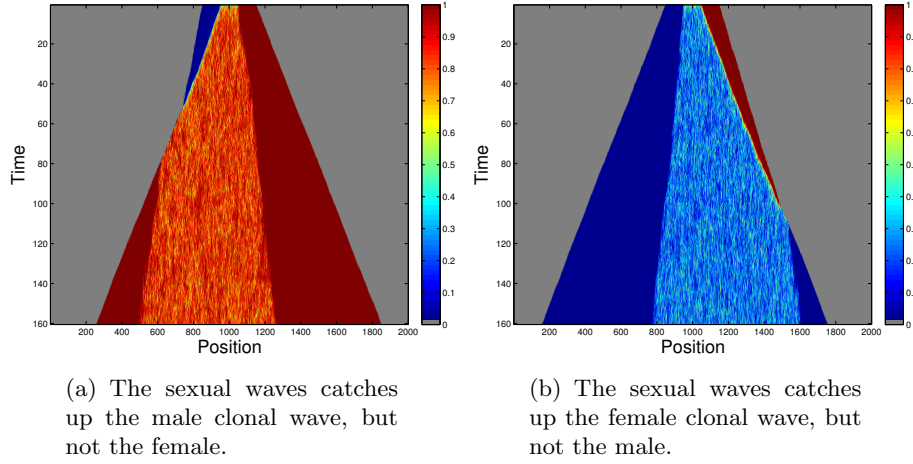
Figure 3.12: The speed of the clonal and sexual waves and their implications on colonization. In the left panel a sexual wave catches up female clonal waves, but not male clonal waves, and colonization goes in the form of two female clonal waves. In the right panel the opposite holds. The clonal birth rates are in the left panel $c_f = 5$, $c_m = 15$ and in the right panel $c_f = 15$, $c_m = 2$. Other parameters are in both panels: $s = 40$, $\sigma = 2$, $K = 10$. The initialization was "Male-Both-Female". For color notation and initialization, see the beginning of Section 3.2.

Starting from a founder colony of both sexes, clonal waves can break away from the region with sexual reproduction if they move with higher speed than the sexual wave. This has already been seen in Figure 3.12, but is better illustrated in Figure 3.13 where two clonal waves, one female and one male, break away from a region with both sexes and colonizes empty habitat.

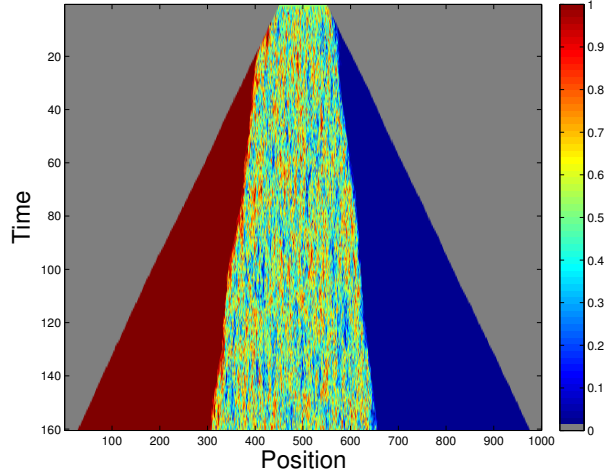*Figure 3.13: Clonal waves breaking away from sexual regions. Parameters: $s = 50$, $c_f = 50$, $c_m = 50$, $\sigma = 1$, $K = 10$. The initialization was "Uniform-middle". For color notation and initialization, see the beginning of Section 3.2.*

3.2.6   The trivial steady states

In Section 3.2.3, sexual waves were introduced. These waves can invade clonal regions, replacing the latter with sexual regions. The sex ratio achieves its (non-trivial) stable steady-state locally through this invasion.

However, there are parameter settings that forbids a non-trivial steady state and implies that fixation of one of the sex is the stable steady state (see Section 3.1.4). With the same reasoning as in Section 3.2.3, this must imply that, instead of a sexual wave, we have a wave that brings fixation of the sex with highest clonal birth rate. We introduce the notation *fixating wave*, for the wave that replaces an unstable fixation with a stable fixation. We must conclude that there are two kinds of fixating waves:

- A female fixating wave if $c_f - c_m \geq \frac{s}{2}$.

- A male fixating wave is $c_m - c_f \geq \frac{s}{2}$.

Within time, a fixating wave spreads over the entire habitat, and global fixation of the sex ratio is achieved. This global fixation of the sex ratio is a trivial steady state of the population, and it is stable if the parameters forbid a non-trivial steady state. Thus the trivial steady states for the spatially explicit model are analogous to the trivial steady states of the well-mixed model. The spreading of trivial steady states through fixating waves is shown in Figure 3.14.

(a) Stable steady state: All fe-
males.

(b) Stable steady state: All
males.
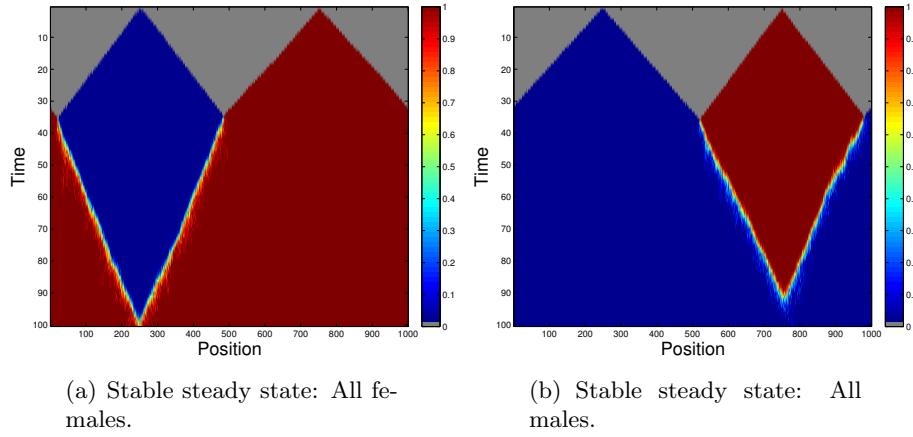
Figure 3.14: Trivial steady states spreading over the habitat as fixating waves. The clonal birth rates are in the left panel $c_f = 50$, $c_m = 20$ and in the right panel $c_f = 20$, $c_m = 50$. Other parameters are in both panels: $s = 20$, $\sigma = 3$, $K = 10$. The initialization was "One male, one female". For color notation and initialization, see the beginning of Section 3.2.

3.2.7   The non-trivial steady state

If we have a non-trivial steady state, sexual waves will eventually bring sexual reproduction and both sexes to the entire habitat. In this way there is a non-trivial steady state for the spatially explicit model that is analogous to the non-trivial steady state for the well-mixed model. Figure 3.15 shows how the non-trivial steady state is reached from an initialization with only clonal colonies.
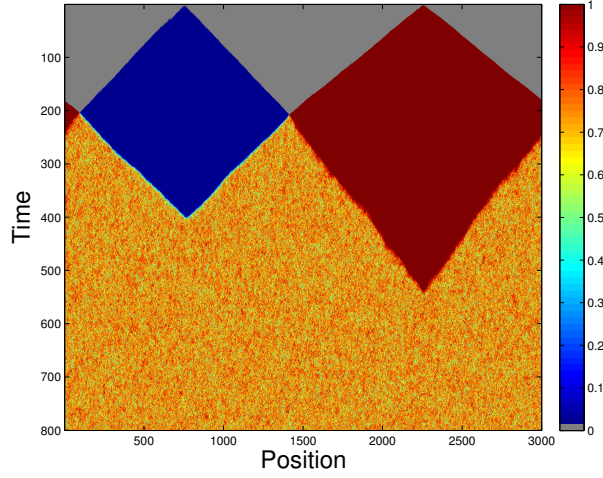
Figure 3.15: The spatially explicit model reaches the non-trivial steady state (continuation of the realization in Figures 3.7 and 3.8). The steady state is reached around generation 560, when the female clonal colony was fully replaced. For color notation, see the beginning of Section 3.2.

The non-trivial steady state of the spatially explicit model is reached when a certain sex ratio with both sexes is spread over entire habitat. Analogous to the well-mixed case, the sex ratio will fluctuate around the non-trivial steady state both locally and globally. From the well-mixed model, we can expect the average global frequency of females to be

$$x_f^* = \frac{1}{2} + \frac{c_f}{s} - \frac{c_m}{s}.$$ (3.10)

This is a good approximation for a large set of parameters. Figure 3.16 shows that, when the effects of fluctuations are small, the non-trivial steady state of the spatial model is indeed very well described by Equation (3.10). However, fluctuations together with the asymmetry described in Section 3.2.4 cause deviations from this prediction. The reasons for these deviations are explained in the following.
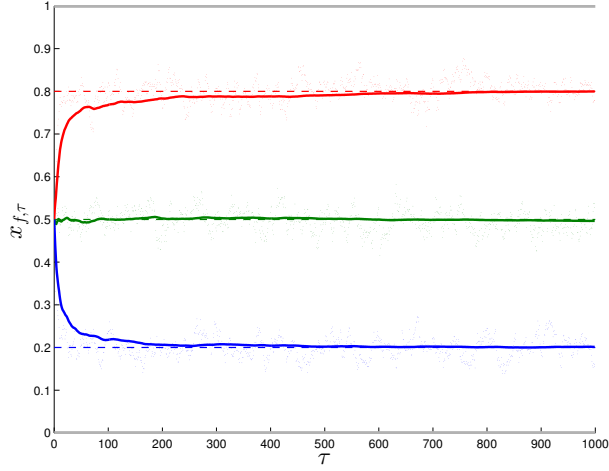
Figure 3.16: Global sex ratio in the non-trivial steady state of the spatially explicit model when the effect of fluctuations are small. Dots are $x_{f,\tau}$, and the solid lines are their cumulative mean. Dashed lines are the steady states predicted with Equation (3.10). Red color is $c_f = 130$, green color is $c_f = 100$ and blue color is $c_f = 70$. Other parameters are for all colors: $c_m = 100$, $s = 100$, $\sigma = 10$, $M = 100$, $K = 10$.

Large fluctuations can cause a population in the non-trivial steady state to consist partly of clonal regions, an effect that is further described in the next section. If fluctuations are large, the the dominating sex will form clonal regions to a higher extent and gain even more ground. In this way, fluctuations cause a shift of the sex ratio and this effect is shown in the left panel of Figure 3.17.

The dispersals taking place are not symmetrical between the sexes as was described in Section 3.2.4. This asymmetry cause sexual reproduction to invade female clonal colonies more than male clonal colonies if the clonal birth rates are equal ($c_f = c_m$). Thus, if the steady state consist of clonal regions and c_m equals c_f, there will be a shift of the non-trivial steady state towards containing more males than females. This shift is seen in the right panel of Figure 3.17.

(a) Effect of dominant sex gain-
ing ground.

(b) Effect of asymmetry in dis-
persals.
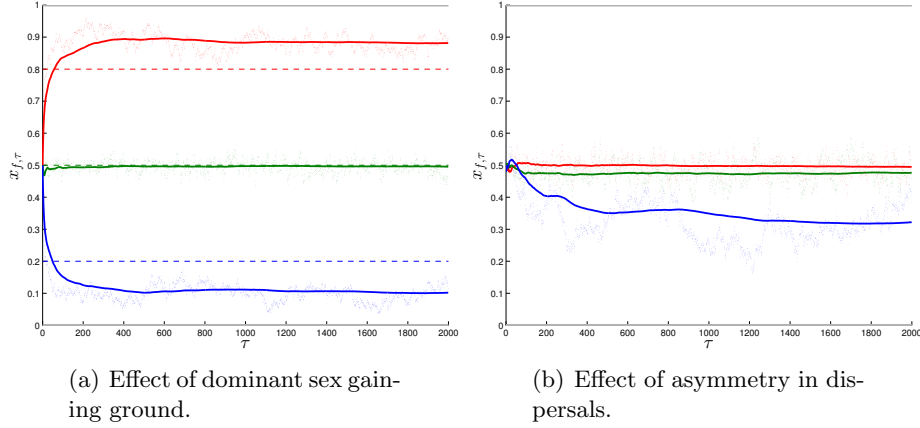
Figure 3.17: Deviations from the sex ratio predicted in Equation (3.10), an equation motivated from that the dynamics in the spatially explicit model resembles the dynamics in the well mixed model. However, when fluctuations are large, the prediction can fail for two reasons; due to a dominant sex forming clonal regions and/or due to the asymmetry in dispersals between the sexes. In the left panel, deviations are due to the former, and in the right panel they are due to the latter. Dots are $x_{f,\tau}$, and the solid lines are their cumulative mean. Dashed lines are the steady states predicted with Equation (3.10). Colors denote in the left panel: Red: $c_f = 130$, green: $c_f = 100$, blue: $c_f = 70$. Other parameters are for all colors in the left panel: $c_m = 100$, $s = 100$, $\sigma = 10$, $M = 2000$, $K = 1$. Colors denote in the right panel: Red: $\sigma = 10$, green: $\sigma = 3$, blue: $\sigma = 2$. Other parameters are for all colors in the right panel: $c_f = 100$, $c_m = 100$, $s = 100$, $M = 1000$, $K = 1$.

3.2.8 Effect of fluctuations

It was mentioned in Section 3.2.3 that the sexual wave can be interrupted by fluctuations. Another effect of fluctuations is also present after the sexual wave has passed - in the non-trivial steady state. Here fluctuations cause the sex ratio to vary over space and time.

Fluctuations increase with decreasing σ, K, and s, and increasing c_f and c_m. Low values of σ and K imply that an individual interacts nearby and is surrounded by a low density of neighbors; the groups of communicating individuals are small, and fluctuations have a large effect on each such group. This is analogous to that fluctuations are larger in the well-mixed model when the population size, N, was small (see Section 3.1.5).

For both the spatially explicit and the well-mixed model, it is sexual reproduction that drives the sex ratio towards a non-trivial steady state. This is the reason for that fluctuations are increased by increasing c_f and c_m and decreased by increasing s. In Figure 3.18, the increase of fluctuations

with decreasing s and σ is shown. We see both small and large effects of fluctuations and that fluctuations cause variation of the sex ratio over space and time.

(a) High s, high σ

(b) Low s, high σ

(c) High s, low σ

(d) low s, low σ
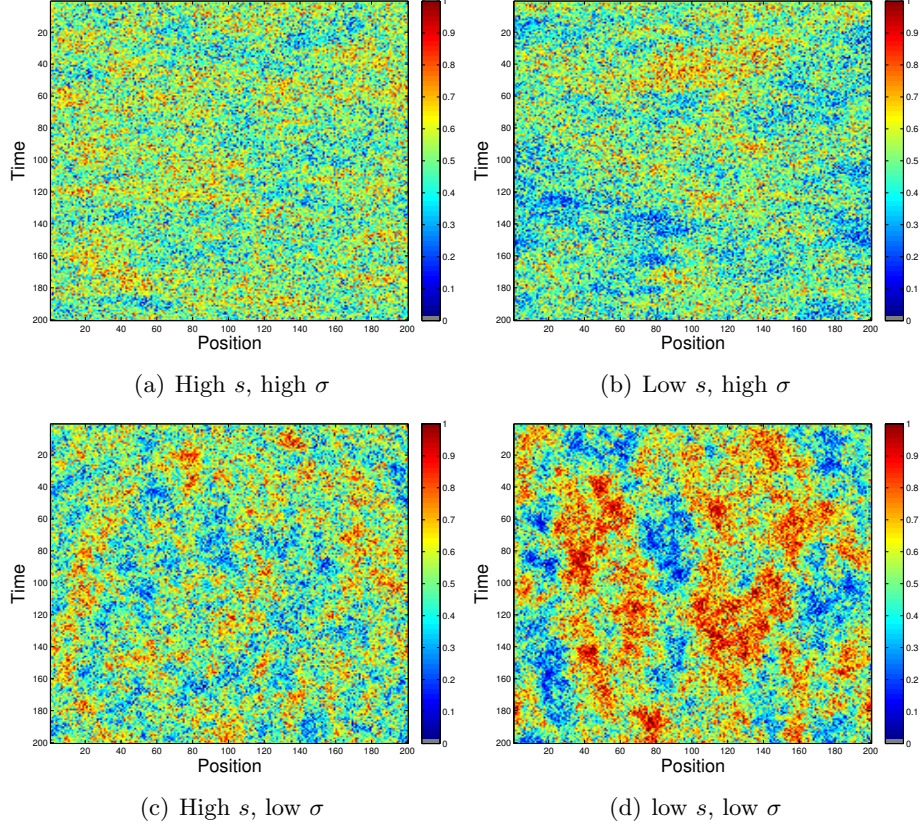
Figure 3.18: Fluctuations causing the sex ratio in the non-trivial steady state to vary over space and time. The effect of fluctuations increase with decreasing s and σ. Low s refers to $s = 10$, high s refers to $s = 50$. Low σ refers to $σ = 2$, high σ refers to $σ = 6$. Other parameters are in all panels: $c_f = 100$, $c_m = 100$, $K = 10$. The initialization was "Uniform". For color notation and initialization, see the beginning of Section 3.2.

In Figure 3.18 the clonal birth rates were equal for males and females ($c_f = c_m$). As described in Section 3.2.7 this implies a sex ratio that, after a the non-trivial steady state is reached, fluctuates around $x_f = 1/2$.

Also if we have a non-trivial steady state in which one sex is more frequent than the other, the sex ratio fluctuates around it and causes variation over space and time. This is exemplified in Figure 3.19.

(a) $c_f = 101$, $c_m = 100$ (b) $c_f = 100$, $c_m = 101$

Figure 3.19: Variation of the sex ratio over space and time around a steady state that is shifted towards domination of one sex. In the left panel, the steady state is shifted towards more females than males. The opposite holds for the right panel. The values of c_f and c_m are shown for each panel. Other parameters are in both panels: $s = 10$, $\sigma = 3$, $K = 10$. The initialization was "Uniform". For color notation and initialization, see the beginning of Section 3.2.
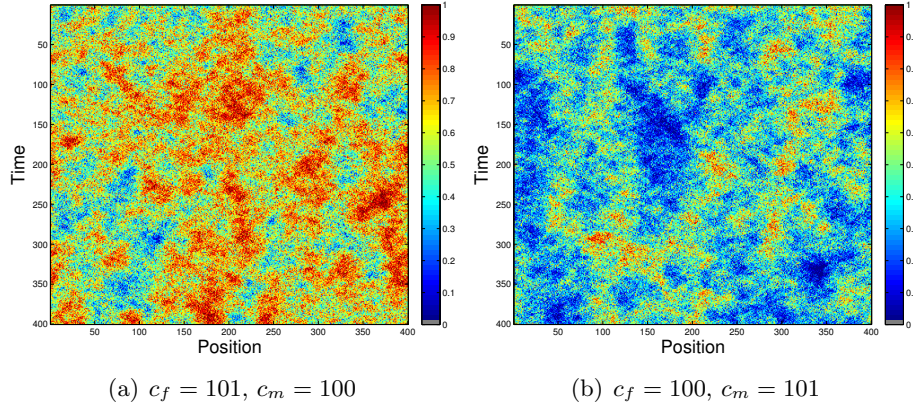
We have seen that fluctuations cause the sex ratio in the non-trivial steady state to vary over space and time. This can be understood from the effect of fluctuations on local communicating groups. In the following we will see that, when fluctuations are large enough, they can imply loss of one sex in a communicating group, and cause reproduction to be purely clonal locally. Analogously to as in the well-mixed model, where the time to loss scales exponentially with the population size, such a loss happens frequently if the communicating groups are small.

Clonal regions can spread into sexual regions when a sex is lost due to fluctuations in the sexual region. The spreading of clonal regions is counteracted by invasion of sexual reproduction that re-implants the lost sex. Therefore, if fluctuations are large, the steady state with variation of sex ratio over space and time consists of local populations with only one sex where reproduction is purely asexual. These local populations remind of islands in the habitat in that they are surrounded by regions where both sexes are present, and where sexual reproduction persists. They will therefore be referred to as *clonal islands*. Just as they are an extreme case of a non-trivial steady state where the sex ratio varies over space and time, the clonal islands move, grow and shrink over time. In Figure 3.20 both female and male clonal islands, surrounded by sexual regions, are seen.
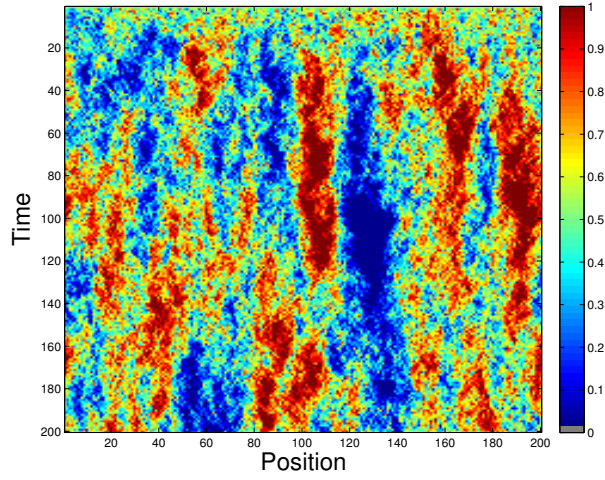
Figure 3.20: Fluctuations giving rise to clonal islands. Both female and male clonal islands occur. Parameters used: $s = 5$, $c_f = 150$, $c_m = 150$, $\sigma = 1$, $K = 10$. The initialization was "Uniform". For color notation and initialization, see the beginning of Section 3.2.

Using different clonal birth rates for females and males ($c_f \neq c_m$), the non-trivial steady state is shifted towards containing more individuals of the sex that is better at cloning. This dominating sex is more likely to establish clonal islands than the other. In Figure 3.21 two examples are shown, one displays female clonal islands dominating over male clonal islands and the other displays the opposite. Furthermore, in Section 3.2.7 it was explained how this effect enhances a shift of the global sex ratio.

(a) Female clonal islands dominate.

(b) Male clonal islands dominate.
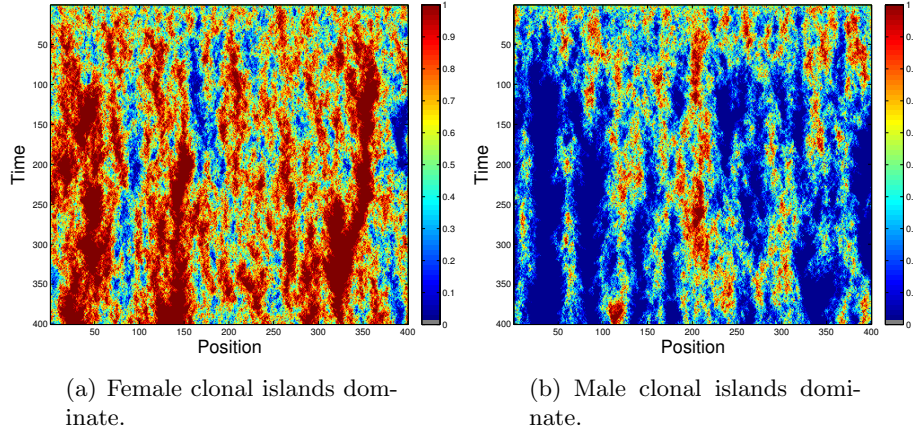
Figure 3.21: Fluctuations giving rise to clonal islands. In the left panel female clonal islands are dominating over male clonal islands, in the right panel the opposite holds. Clonal birth rates are: $c_f = 152$, $c_m = 150$ (left panel) and $c_f = 150$, $c_m = 152$ (right panel). Other parameters are in both panels: $s = 10$, $\sigma = 1$, $K = 10$. The initialization was "Uniform". For color notation and initialization, see the beginning of Section 3.2.

3.2.9 Genetics

As was motivated in Section 2.2, every sexual offspring is assigned a unique genotype, and a clonal progeny is assigned the same genotype as its (asexual) parent. Since clonal reproduction does not produce any new genotypes, the genetic diversity is higher in regions where sexual reproduction takes place than in purely clonal regions. Figure 3.22 shows the genetics for the realization for which the sex ratio was shown in Figures 3.7, 3.8 and 3.15. We note that it is the sexual wave that introduces new genotypes.

(a) Sex-ratio. (b) Genetics.

Figure 3.22: Comparison between sex ratio and genetic variation (the same realization as in Figure 3.15). Left panel: sex ratio, right panel: number of unique genotypes. The clonal colonies consist of only one genotype and diversity is brought by the sexual wave. For color notation, see the beginning of Section 3.2.

If the parameters allow for a clonal wave to break away from a sexual region (see Section 3.2.5), then this clonal wave consists of only one genotype. This is shown in Figure 3.23, where one female and one male clonal wave break away from a region with both sexes present.

(a) Sex-ratio.
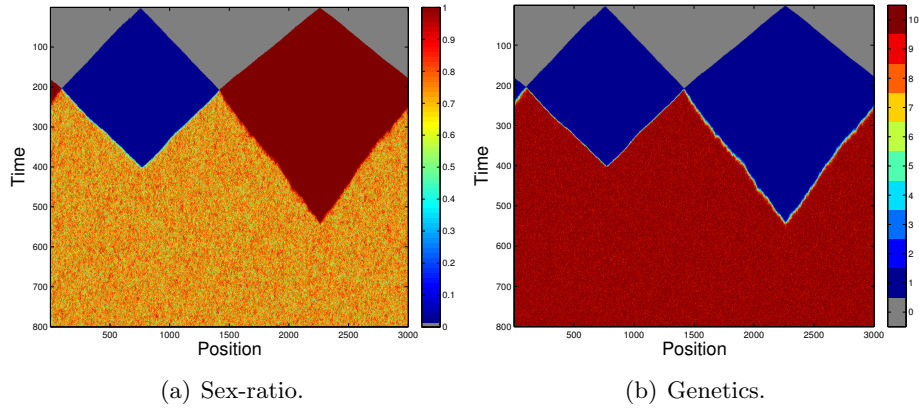
(b) Genetics.

Figure 3.23: Comparison between sex ratio and genetic variation (the same realization as in Figure 3.13). Left panel: sex ratio, right panel: number of unique genotypes. The clonal waves that break away from the sexual region consist of only one genotype. For color notation, see the beginning of Section 3.2.

Sexual waves that are interrupted by fluctuations that cause previously sexual regions to be replaced by asexual (see Section 3.2.3), leaves genetic traces; allowing multiple clones of the same sex to coexist. This effect is shown in Figure 3.24.

(a) Sex-ratio.
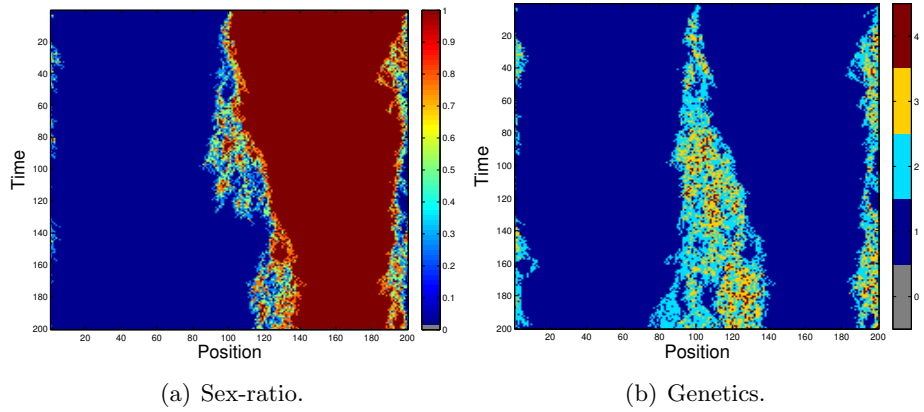
(b) Genetics.

Figure 3.24: Comparison between sex ratio and genetic variation (the same realization as in the left panel of Figure 3.9). Left panel: sex ratio, right panel: number of genotypes. The sexual reproduction that was lost due to fluctuations has left a trace of genetic diversity in a male clonal region. For color notation, see the beginning of Section 3.2.

Traces of genetic diversity are also seen in the wake of fixating waves (see Section 3.2.6). The sexual reproduction taking the sex ratio to the trivial

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steady state produces new genotypes. There will be multiple genotypes of only one sex in the same cell after a fixating wave has passed. This effect is shown in Figure 3.25.

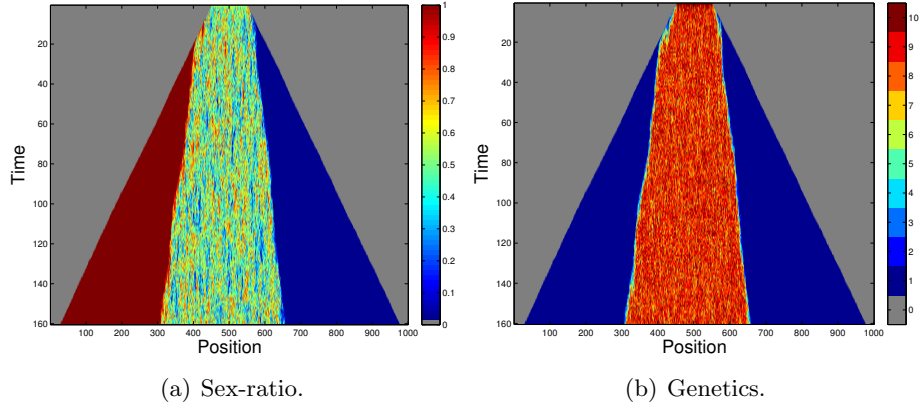(a) Sex-ratio.   (b) Genetics.
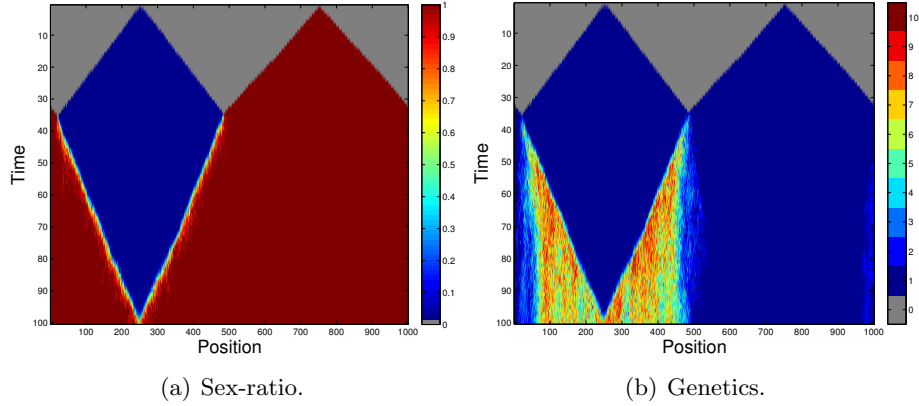
Figure 3.25: Comparison between sex ratio and genetic variation (the same realization as in the left panel of Figure 3.14). Left panel: sex ratio, right panel: number of genotypes. The sexual reproduction that took place at the front of the fixating wave leaves a trace of genetic diversity in a female clonal region. For color notation, see the beginning of Section 3.2.

In section 3.2.8 it was described how fluctuations yield a non-trivial steady state with a population that partly consists of clonal islands. Since no new genotypes are formed in the clonal islands, their genetic diversity will be low compared with the diversity in sexual regions. This effect is shown in Figure 3.26.

(a) Sex-ratio.
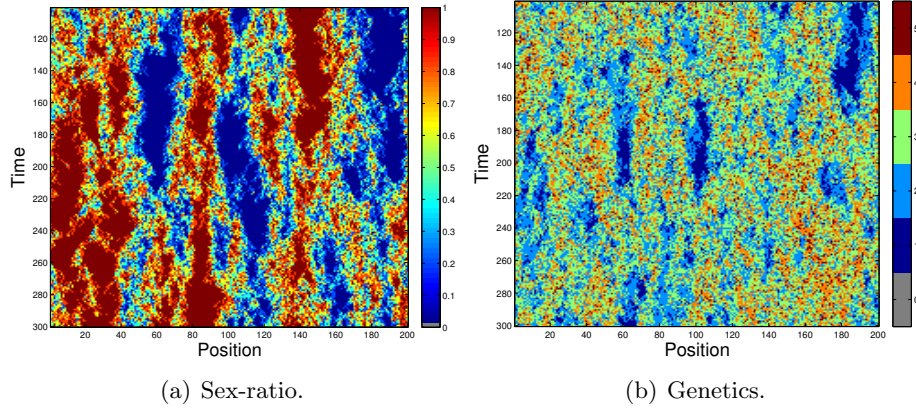
(b) Genetics.

Figure 3.26: Comparison between sex ratio and genetic variation for a realization with female and male clonal islands. Left panel: sex ratio, right panel: number of genotypes. Fluctuations giving rise to clonal islands affects the genetic diversity; less genotypes are found in the clonal islands than in sexual regions. Parameters: $c_f = 100$, $c_m = 100$, $s = 10$, $\sigma = 1$, $K = 5$. The initialization was "Uniform". For color notation and initialization, see the beginning of Section 3.2.

4 | Discussion

In this thesis, I have studied the dynamics of the sex ratio and the genetics for populations with mixed sexual and asexual reproduction by means of computer modeling. In this chapter I first discuss how my results relate to biological populations in general. Secondly, how the results relate to populations *F. radicans* in particular is discussed.

In populations of *F. radicans* as well as of other species, sperms traverse longer distances than eggs. This has inspired me to formulate a hypothesis concerning the consequences for an such asymmetry between the sexes - *The Range hypothesis* - to which a separate section is dedicated. There remain many interesting questions to answer for populations with mixed sexual and asexual reproduction, not least for *F. radicans* populations. An outlook concerning the future applications of computer modeling in the field is provided.

4.1   Main conclusions

The results presented in this thesis provide insight into properties and mechanisms that can be important for populations of *F. radicans*, but also for other populations that reproduce both sexually and asexually. In summary:

- There are three possible cases for the steady state of the sex ratio, with specific conditions for each case.

- Colonization of empty habitat can proceed as a clonal wave that forms clonal colonies of only one genotype.

- A sexual wave can invade clonal colonies and bring genetic variation and a state where both sexes coexists. There are specific conditions for a sexual wave to occur.

- Fluctuations counteract the effect of a sexual wave, and can induce clonal islands in previously sexual regions.

4.1.1 The stable steady states of the sex ratio

In both models, there are three possible cases for the stable steady state of the sex ratio; all females, both sexes and all males. Which steady state that is eventually approached depend on the parameters c_f, c_m and s (for the explicit dependence I refer to Section 3.1.4). In summary:

If the clonal birth rates in males and females are not exactly equal, the sexual reproduction must exceed a certain threshold, for the population to escape fixation of the sex that is more prone to cloning.

The main counter-argument for this result is that it is a consequence of how the models were designed. I now argue that this is not the case.

The questions is really: What is expected to happen when an individual lives with only neighbors of the other sex? Let us for clarity assume that a male lives with only female neighbors. If the expected number of males in the next generation is > 1, then fixation of females is an unstable steady state. If the expected number of males is < 1, then fixation of females is a stable steady state.

The expected number of males in the next generation must increase with the male clonal birth rate and decrease with the female clonal birth rate. Sexually reproduced individuals can be of both sexes, and if male and female sexual offspring are born in equal proportions, increased sexual reproduction will drive the expected number of males towards a higher value than unity. Even if sexually reproduced individuals are biased towards males, there is no guarantee that this will compensate for a female clonal birth rate that is higher than the male clonal birth rate. Similarly, there is no guarantee that a female with only male neighbors by necessity should imply that the expected number of females in the next generation is > 1.

In any reasonable, well-mixed and genetically neutral model, the frequency of females must update according to some function f. In the deterministic limit, the updating is given by:

$$x_f \leftarrow f(x_f; \Omega), \tag{4.1}$$

where Ω is a set of parameters. We now investigate the stability of the fixated states; Are $f(\delta x_f; \Omega) > \delta x_f$ and/or $f(1 - \delta x_f; \Omega) < 1 - \delta x_f$ for some small $\delta x_f > 0$? If the first condition is met, fixation of males is an unstable steady state. If the second condition is met, fixation of females is an unstable steady state. A condition that is not met corresponds to fixation being stable.

The conditions can be investigated by linearizing around the states $x_f = 0$ and x_f, and take the derivative as the derivative for $x_f \leftarrow 0+$ and $x_f \leftarrow 1-$.

Thus, if

$$f'(0; \Omega) > 1 \quad \text{and} \quad f'(1; \Omega) > 1, \tag{4.2}$$

then we must have (at least) one non-trivial stable steady state. I claim that there is no guarantee that the conditions in (4.2) will always be met in reasonable models, especially when the amount of sexual reproduction is low. Nature is full of asymmetries between sexes, and such asymmetries can cause qualitative differences for the steady states of the sex ratio between populations. It is thus problematic to discuss populations with mixed sexual and asexual reproduction and assume that both sexes will always be present. On the contrary: if both sexes are present, this gives some information of how frequent sexual reproduction is and of that the clonal birth rates can not differ too much between females and males.

Example

Let us clarify the reasoning above by an example. We will now investigate a model that is identical to our well-mixed model, except for that the number of sexual offspring born is given by another expression. The number of sexual offspring is now given by

$$N_{sexual} = s_f N_f \left(1 - e^{-s_m \frac{N_m}{N}}\right), \tag{4.3}$$

where s_f corresponds to the number of eggs that a female produces and s_m corresponds to the number of sperms that a male produces and the probability for a sperm to fertilize an egg. N_f and N_m are the number of females and males respectively. Equation (4.3) is a saturating formula that could mirror that the sperms outnumber the eggs, and that it is the number of eggs that limits the number of sexually born offspring. Except for the new formula for the number of sexual offspring, this temporary example is identical to the well-mixed model.

With this example we arrive to that

$$f(x_f; c_f, c_m, s_f, s_m) = \frac{c_f x_f + \frac{1}{2} s_f \left(1 - e^{-s_m(1 - x_f)}\right)}{c_f x_f + c_m(1 - x_f) + s_f \left(1 - e^{-s_m(1 - x_f)}\right)} \tag{4.4}$$

with

$$f'(0; c_f, c_m, s_f, s_m) = \frac{c_f + \frac{1}{2} s_f \left(1 - e^{-s_m}\right)}{c_m}$$

$$\text{and} \tag{4.5}$$

$$f'(1; c_f, c_m, s_f, s_m) = \frac{c_m + \frac{1}{2} s_f s_m}{c_f}.$$

We find that females are expected to invade an all male colony if and only if

$$c_m - c_f < \frac{1}{2}s_f \left(1 - e^{-s_m}\right),\tag{4.6}$$

and that males are expected to invade an all female colony if and only if

$$c_f - c_m < \frac{1}{2}s_m s_f.\tag{4.7}$$

We note that, also for this example, the existence of a non-trivial stable steady state depends on that the difference in clonal birth rate between males and females is not to large, and that sexual reproduction is high enough. If the sexual reproduction is below a certain threshold, the population is driven towards a state where only the sex that is better at cloning persists.

4.1.2 Clonal and sexual waves

The dynamics of the sexes in the model[1] provide a reaction-diffusion system with four or three stationary solutions[2]. The solution to such systems are traveling wave fronts that connects the stationary solutions; clonal waves that connects empty habitat with populated, and sexual (and fixating) waves that connects an unstable fixation with the stable steady state.

There are two aspects to consider as far as these waves are concerned; the parameters that allow for them, and the speed at which they travel. In reality, "parameters", correspond to properties of a species together with its living conditions at the location of the wave. If a sexual wave invades a clonal colony faster than the clonal colony expands (see right panel of Figure 3.11), clonal waves are not to be expected to arise from a region where both sexes exist. Clonal waves can however still be expected if only one sex is present in empty habitat, in the case of *F. radicans* perhaps due to an individual that was moved by storms. If, on the other hand, the clonal waves travel faster than the sexual waves, the colonization will go in the form of a clonal wave that is followed by a sexual wave at a later time (see Figure 3.13).

In the model, the speeds of the female and male clonal waves increase with their clonal birth rates and the dispersal range of clonal branches, a feature that can also be expected in reality. An increased clonal birth rate stabilizes a clonal colony, and can slow down the sexual wave. But increased clonal birth rate in the sex that is not in the clonal colony should increase the speed of the sexual wave; if a mixed situation invades an all female colony,

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[1]Waves are only found in the spatially explicit model, and when referring to "the model" in this section we refer to this one.

[2]The stationary solutions are: 1) Empty habitat, 2) Fixation of females, 3) Fixation of males , and 4) The non-trivial stable steady state (if it exists).

more males will compete if the clonal birth rate for males is increased. In the model this feature is observed, and I find it hard to imagine that it would not be the case in reality.

In our model, the dispersal range was assumed to be identical for sperms, zygotes and clonal offspring. This is a problematic approximation of the situation in real populations since, typically, sperms disperse over larger ranges than the other elements. From my understanding of the model I however think that the sexual waves would still be observed even if sperms dispersed over a larger range. The speed of the sexual wave into female clonal regions would be increased, and its edge would be less sharp since some sperms runs ahead of it and inserts males into the previously clonal region. The chance of a female clonal wave to run ahead of the sexual wave is reduced, but the possibility remains, especially if the amount of sexual reproduction is low.

A male that emerges in a female clonal colony due to long-range dispersal of sperms is assigned the same properties as as any other male individual. From this point of view, an increased dispersal range of sperms is similar to setting all dispersal ranges to that of sperms, or to introducing rare relocations over a larger spatial scale. Therefore, the less sharp edge of the wave into female clonal regions is the main consequence I can see of an increased range of sperm dispersal. With such a "rough edge" of the sexual wave, other genotypes regularly interrupts the colonizing clone during a transient phase. This consequence can however be important since it contains a possible explanation for the genotypic patterns observed for *F. radicans*. In the Outlook, I suggest the consequences of a larger range of sperm dispersal as a topic for future research.

It is important to keep in mind that Nature is much more complex than our model. In our model, the living conditions for the population are identical in all the habitat; the parameters are the same everywhere. In nature, this is likely not the case. It is easy to imagine that local conditions makes, for instance, sexual reproduction more beneficial at some places and less beneficial at some.

My conclusions suggest that we should take into consideration that, in nature, we might find different dynamics at different locations. If sexual reproduction is low at some location, the sex ratio might be driven towards fixation there, while this is not the case at other locations. The speed of the sexual wave might be lower than that of the clonal waves at some locations, but higher at some. Thus, some regions will be colonized through cloning, and some will be colonized through sexual reproduction.

It was shown in Section 3.2.5 that there are parameters for which the clonal wave of one sex is caught up by the sexual wave, whereas the clonal wave of the other sex escapes. This implication was natural to illustrate

when explaining the results, but I leave it to biologists to consider the relevance for real populations. To explain clonal colonies where only one sex is observed, different speeds of the female and male clonal wave could be considered. As mentioned, typically sperms traverse longer distances than eggs in real populations, but the consequences of this has not been explored in our model. One must however expect that this provides a mechanism that could forbid female clonal waves, but still allow for male clonal waves.

In biological populations, genetic variation increases with increasing sexual reproduction, due to recombinations. The main mechanism for cloning to cause a new genotype is through point mutations, and this effect was assumed negligible when genetics were simulated. Recombinations allow for a vast set of genotypes from a limited set of genetic material, and thus sexual reproduction was assumed to give rise to a unique genotype. The increased genetic variation from sexual reproduction is observed in our model (see Section 3.2.9), where regions with only one sex has less diversity than regions with both sexes. Especially in Figure 3.22, it is the sexual wave that causes genetic variation.

In Figure 3.25 it is seen that a fixating wave leaves a trace of diversity in clonal regions due to earlier sexual reproduction. Since no advantage is assigned to any genotype, the genotypes in clonal regions are subject only to diffusion. Genotypes are occasionally lost due to fluctuations, and no new genotypes are introduced in clonal regions. This is the mechanism that cause clonal regions to loose genetic variation with time, and therefore clonal islands consist of relatively few genotypes (seen in Figure 3.26). Losses of genotypes must be expected in reality, and I think our model mirrors this aspect well.

4.1.3   Fluctuations

The fluctuations modeled are purely so called *demographic fluctuations* - fluctuations due to random events in a constant environment. *Environmental fluctuations* are the contrary to demographic fluctuations - fluctuations in a population caused by changes in the environment. Adding environmental fluctuations to the models would complicate them, and for this reason it was not done; The first priority was to understand the dynamics with only demographic fluctuations and neglect environmental fluctuations.

However, we can already predict some outcomes of environmental fluctuations. If, for instance, low temperature caused sexual reproduction to fail completely in one generation, we have insight into what the consequences are: the population is modeled by setting he parameter s set to zero that specific year. If, in one generation, all individuals die out locally, we have already modeled how the, now empty, habitat is colonized. What is not explored are the effects of stochastic and re-occurring changes of the envi-

ronment.

The demographic fluctuations caused a sex ratio that varies over space and time, and for large fluctuations clonal islands could emerge. Fluctuations, especially large, had effect on the genetics. It is hard to estimate the relevance of demographic fluctuations for real populations. Would reality correspond to small effects of fluctuations - that fluctuations cause some variations but these variations are without important consequences? Or are the effects of fluctuations large, so that clonal islands are formed frequently?

For our models, we know which parameters that increase the effects of fluctuations (high c_f and c_m) and which parameters that decrease them (high K and s), and analogy between the effects of the parameters and effects in reality is to be expected. It might be so that, locally, the sexual reproduction is low in relation to clonal, with the implication that fluctuations are of importance there, but not elsewhere. For *F. radicans*, there might be local populations that live in turbulent waters that cause dispersals of gametes, zygotes and adventitious branches to be longer than elsewhere. The effects of fluctuations would then be reduced for these populations.

I leave the question open whether demographic fluctuations are of importance for a specific species. Their presence should however be expected, since nature is neither continuous or deterministic. I have presented how their effects can be increased with increasing clonal and decreasing sexual activity. I have shown that the effects of fluctuations are increased with smaller population size for the well-mixed model and with smaller size of the communicating groups in the spatially explicit model. These correlations can be expected for any biological population, but the consequences of demographic fluctuations could be more or less drastic.

One can picture a situation where demographic fluctuations become important if they are combined with environmental fluctuations. In the earlier example, where the sexual offspring died out due to low temperature a specific year, demographic fluctuations become more important this year. That year's events can then change the trajectory of future generations and have important consequences, for instance if one of the sexes are lost.

4.2 *Fucus radicans*

The conclusions drawn from the models are relevant for understanding the patterns observed in populations of *F. radicans*. From what is known about the biology of the species, the models are approximations of real processes.

The impact of different clonal birth rates in males and females has been explored. As argued in Section 4.1.1, the qualitative outcome is general; The

population will approach a sex ratio where the sex that is best at cloning dominates, and domination of a sex is counteracted by sexual reproduction. Sexual reproduction must exceed a certain threshold if the sex that is better at cloning should not be driven towards fixation.

In the light of the sex ratio observed in *F. radicans* populations, these results are highly important. At some locations females are more numerous than males, whereas some locations have an equal distribution, and a few locations are dominated by males. In some regions, the species is expected to reproduce clonally to a large extent (corresponding to an s that is low in relation to c_f and c_m), and therefore a slight difference in clonal birth rates has a large impact. It would therefore be of great importance to asses whether there exists such a difference in clonal birth rates. To verify the existence of a slight difference is likely a hard challenge. This raises a problem, since I have shown how a, seemingly negligible, difference can determine the fate of the population.

The clonal and sexual birth rates have consequences for the waves. Sexual and fixating waves takes the sex ratio to the stable steady state. Clonal waves can cause one genotype to dominate, even if it does not have a higher fitness. It is however problematic to explain the observed superfemale with the waves occurring in our spatially explicit model. A clonal wave brings only one genotype, and variation is brought by the sexual wave. However, the sexual wave tends to remove the dominance of the founding genotype, and bring a situation whit many coexisting genotypes without any particular dominance. This points to that the explanations for the observed pattern lies in mechanisms that were neglected in our models.

The spatially explicit model assumes neutral fitness, and that dispersed elements (sperms, eggs and adventitious branches) are dispersed over the same length scale. I think that the answer to the observed pattern lies in abandonment of one or both of these assumptions. If the superfemale has a slightly higher fitness than other genotypes, the answer might lie there. I however think that important clues can be found when modifying the dispersal ranges.

When comparing to the biology of *F. radicans*, one must conclude that the dispersals modeled are realistic on the short range. Most reproduction is local and therefore all dispersals regarding them can be modeled with the same Gaussian function. One must however expect dispersals to sometimes, perhaps rarely, be on a larger length scale. Such events have the potential to initiate the local processes demonstrated in our spatially explicit model at a new location; a clonal branch or zygote dispersed to empty habitat initiates a clonal wave, and a sperm dispersed into a female clonal region can initiate a sexual wave there. Kleinhans et. al. have shown how rare "relocations" with a large range could lead to colonization by clonal waves despite assigning a higher effectiveness to sexual reproduction [12].

If the reason for the superfemale does not lie in a higher fitness, it is reasonable to assume that she gained dominance by being first at place. I can see no other explanation under fitness-neutral assumptions. Then remains to explain how she can dominate, while coexisting with other genotypes. If the superfemale colonized empty regions as a clonal wave, explanations might be that:

- Sperms that were dispersed over a long range occasionally initiated sexual waves in the superfemale.

- Occasional long-range dispersals of adventitious branches and/or zygotes made colonization go in the form of clonal waves initiated at many locations. This caused some genotypes to be numerous and widespread, especially the superfemale that gained domination (see [12]).

- Occasional hybridization with the sister species, *F. vesiculosus*, gave fertile offspring that initiated sexual waves locally.

- At some locations, the conditions for sexual reproduction were so bad, that the sexual wave could not invade there. It might be so that a sexual wave will never consume the superfemale at these locations, or that the sexual wave invades exceptionally slowly. Therefore the superfemale is preserved, and can constantly re-implant her genotype into her neighboring regions.

It might very well be the case that the explanation for the genotypic patterns observed lies in more than one of these hypotheses. The three first would in a model all correspond to the introduction of long-range dispersals; a new sex and a new genotype is introduced without interaction with nearby neighbors.

The last hypothesis intrigues me. Nature is highly complex, and we can expect the conditions for reproduction to vary to a large extent. It might for instance be so that, at a certain depth, sexual reproduction is impossible, whereas clonal reproduction is possible. Then these depths would act as a "bank" filled with individuals of the superfemale that regularly clones themselves into regions were sexual reproduction is allowed. With background in this hypothesis and my results concerning the steady state of the sex ratio, increased knowledge in the reproduction in *F. radicans* would be of high importance.

My results show that demographic fluctuations cause the sex ratio to vary over both space and time. These fluctuations can be of importance when explaining the patterns for *F. radicans* shown in Figure 1.2. Even without

differences in fitness, some genotypes are more numerous than others locally, and such a local dominance is eventually lost.

Demographic fluctuations can not alone explain the superfemale. These fluctuations acts after the sexual wave has passed and the genotype that dominate locally due to fluctuations can be any genotype. We can not expect the widespread domination of the superfemale only due to demographic fluctuations. However, effects of fluctuations must to some extent be present, and when combined with other biases towards the superfemale (a slightly higher fitness of the superfemale and/or one/some of the hypotheses listed earlier in this section), they might be of importance.

As mentioned in Section 4.1.3, the consequences of environmental fluctuations were not explored, and the role of them can be important. It was also described how environmental fluctuations may increase the effects of demographic fluctuations.

4.3   The Range-hypothesis

During my work I have on several occasions come to contemplate the real counterpart of the modeled populations - biological populations of *F. radicans* and of other species. I have come to think of mechanisms that are not captured in the models used. If we leave the neutral genetics assumption and allow inheritable properties, which pheno- and genotypes benefits?

In particular, I thought of the advantages and disadvantages of the different reproductive types. Which balance between sexual and asexual reproduction evolves? For populations of *F. radicans* as well as of other species, sperms traverse longer distances than eggs. This asymmetry between the sexes led me to formulate an hypothesis: The Range-hypothesis. This is a general hypothesis for the consequences of a gamete range that differs between the sexes.

The Range Hypothesis:

> Consider a dieoecious population with mixed sexual and asexual reproduction in which sexual reproduction does not imply physical contact, i.e. gametes are released in a medium where fertilization takes place. Assume that, in this population, one of the sexes have gametes that, after releasing, is expected to traverse a longer distance than what is expected for the other sex, i.e. one of the sexes have gametes with a longer range than the other sex has. It is assumed that no kin altruism occurs within this population.
>
> For this population, the difference in range of gametes will cause a tendency for the sex that releases gametes with a longer range to be more prone to sexual reproduction than the sex that releases gametes with a shorter range. Conversely, there will be a tendency for the sex that releases gametes with a shorter range to be more prone to asexual reproduction than the sex that releases gametes with a longer range.

4.3.1   Motivation

The motivation is split up into two parts. First, the hypothesis is motivated from the perspective of evolving organisms. This part gives an intuitive understanding, but it leaves room for doubt, since some complexity is neglected. The second part argues for the hypothesis from the perspective of evolving genes. Here, the limitations of the argumentation in the previous section are easier to handle, and this allows for a general motivation of the Range-hypothesis.

From the perspective of evolving organisms

Let us assume a population with both sexual and asexual reproduction where a male spreads his sperm over a larger area than a female spreads her eggs. This is the case in, for instance, populations of *F. radicans*. A male in this population will have his sexual offspring spread over a larger area than a female will have. The internal competition for space between sexually produced siblings with the same parent is reduced if they are spread over a large area. Thus, if a male is parent to equally many zygotes as a female, the male will have more surviving sexual offspring.

A male is expected to be the parent of equally many zygotes as a female if there are equally many males as there are females. If this is the case, the advantage in reproducing sexually is higher for a male than it is for a female. Organisms live under limited amounts of resources, and an individual that is both sexual and asexual must balance its investments between these repro-

duction types. If we compare the optimal balance for males and the optimal balance for females, we must conclude that there is a relative shift towards sexual reproduction in males, or towards asexual reduction in females. We can expect that such an optimized balance is approached through evolution, and thus the hypothesis.

There would be advantages with dispersals of shorter range if siblings could recognize each other and cooperate, therefore the hypothesis contains a reservation for kin altruism. With no kin altruism, the relative advantage for males should, through evolution, be expected to imply the Range-hypothesis. With everything else equal between the sexes, males would be less prone to cloning and more prone to sexual reproduction when compared to females.

Things get more complicated if there are not equally many males as there are females, especially when you think of the consequences and reasons for this. Reasons for a shifted sex ratio is to be found in a difference in clonal birth rates, a difference that itself can be motivated by the Range-hypothesis. If the sexual offspring of a male competes over a larger area, female clonal colonies are more invaded than male clonal colonies. This could shift the sex ratio towards male dominance. An Individual that belongs to the least numerous sex has a higher advantage in sexual reproduction than an individual that belongs to the most numerous sex. Also, it might be so that the most fit genome codes for sexual offspring to be biased either towards males or towards females. The complexity of populations with both sexual and asexual reproduction cause complications that are hard to overview, but luckily enough, the Range hypothesis can still be defended. I claim that, when arguing from the gene perspective, the hypothesis still stands.

From the perspective of evolving genes

When writing this section it was facilitating to project life, consciousness and a free will to genes and organisms, even though they lack such attributes in reality. Therefore genes are described as agents that "lives", "knows" and "wants", etc ... I hope the reader can cope with this anthropomorphism, and find that it makes the text more accessible.

Populations with mixed sexual and asexual reproduction have at least two choices when spending their resources; to invest in sexual reproduction or to invest in asexual reproduction. There is a choice for each individual; how should it prioritize between sexual and asexual reproduction? We know that the choice for the investments is made under influence of its genes. Genes that maximizes their likelihood to be found in future generations.

Individuals compete and the competition is more critical with neighbors than with individuals far away. There can be advantages in proximity, these are discussed later, but let us for now assume that an individual is better

of lonely than with neighbors, due to less competition. A gene live in such individuals, and is interested in the success of its host. Through the competition between organisms, the genes also compete; the failure or success of a gene depends on the death or success of the organism. But the competition of genes is different. If the neighboring organisms contain the same gene copy, the gene have no interest in that the host competes with its neighbor. The gene does not mind if it host dies as long as the winning organism contains its twin. But a gene that looses in favor of another gene looses its competition and looses ground in future generations. Therefore genes want to compete, but only with genes that are not twins. Competition with twins is waste.

What interest does a gene have in the reproduction of a host? It knows that its host is mortal and therefore its interest is to exist in as many of its offspring as possible. It also wants the hosts offspring to survive and reproduce successfully. However, the interest in survival of the hosts offspring is limited. As mentioned, if the organism killing the offspring contains a twin, the gene cares less than if it does not. The gene want that its future copies are many. But competing with its twins is waste, and therefore the gene also wants its future copies to be spread over a large space.

In an organism the gene acts under influence of the organisms phenotype. It has access to information and can expect itself to be copied into a certain number of clones and a certain number of gametes. It also "knows" that the clones are spread to some extent and that gametes are spread to some extent. According to the previous, the gene benefits if the spreading is over a large space, regardless of whether it is spread in a clone or a gamete. However, for the motivation for the Range Hypothesis, we will just have to remember the benefit from increased spreading of gametes. If gametes are spread more in one of the sexes than they are in the other, this will make sexual reproduction more effective for the gene in that sex than in the other.

When gametes are spread in nature, sperms are usually spread over a larger space than eggs are. Let us for clarity therefore assume that a male spreads his sperms over a larger space than a female spreads her eggs. Let us now remember that the genotype codes for the phenotype. The genes are not necessarily expressed in the same way in all phenotypes, and there can be a general difference in expression between females and males. Since populations with mixed sexual and asexual reproduction displays both types of reproduction there must be advantages in both. But the reproductive strategy, that includes the priority between them, is under influence by the genome.

We can expect that, if sexual reproduction is more effective in males, genes mirror this by an increased priority of sexual reproduction from the priority that would otherwise have been in this sex. Due to limited resources,

this higher priority is on the cost of asexual reproduction. Or vice versa, the shorter dispersal range of eggs provides a mechanism that reduces the priority of sexual reproduction and increases the priority of asexual reproduction. If, one the contrary, a male spreads his sperms over a smaller space than a female spreads her eggs, we would expect the opposite effect; a mechanism that makes the male less prone to sexual reproduction on the cost of asexual and the female more prone.

The reasoning above is done under the assumption that no kin altruism is performed within the population. If kin altruism is performed, a benefit emerges in spreading gametes nearby, and the general conclusion in the hypothesis can not be drawn. However, If individuals benefit from proximity, but can not recognize its own kin, the hypothesis still stands. This is because of the higher benefit for the gene in unrelated individuals spending resources on the wealth of your host, than in related individuals doing it. The help would still be received, and if it is not delivered from relatives this is an advantage rather than a disadvantage.

Genomes that are optimized in respect of gamete range are more optimized than if they are not. Therefore, evolution will drive genotypes to reflect asymmetries in gamete range. This will be expressed phenotypically, and thus the Range Hypothesis can be proposed.

4.4 Outlook

My work is a humble contribution to the knowledge of populations with mixed sexual and asexual reproduction. Many interesting questions to answer remains, not least for *F. radicans* populations. Computer modeling can be a tool in this area, and I dedicate a section to suggest future questions where these can be useful. The models used in this master thesis provides a framework for future modeling, and I therefore propose variations on these that can lead to further knowledge.

4.4.1 Testing the Range-hypothesis

The Range-hypothesis was described in Section 4.3. This hypothesis could be verified with a computer model that shares a lot of features with the spatial model I have worked with. However, a big difference is that, to verify the Range-hypothesis, individuals must be assigned a genome that codes for how it balances its investments between sexual and asexual reproduction. Furthermore, the expression of the genome must differ between female and male individuals.

In Appendix E, I suggest a model that could be used to verify the Range-hypothesis. In this model, the conditions are symmetric between females and

males if the dispersal ranges of sexual investments, σ_e for females and σ_s for males, are equal. If $\sigma_e > \sigma_s$, the range hypothesis predicts that females will be more prone to sexual reproduction than males. If $\sigma_e < \sigma_s$, the opposite is predicted. Therefore, the Range-hypothesis could be tested by plotting the average investments in sexual reproduction for the sexes, $\overline{F}$ and $\overline{M}$, for different combinations of σ_e and σ_s. The Range-hypothesis predicts that $\overline{F} > \overline{M}$ when $\sigma_e > \sigma_s$, and $\overline{F} < \overline{M}$ when $\sigma_e < \sigma_s$.

As seen in Appendix E, I suggest a population distributed over a two-dimensional space rather than a one-dimensional. The reason for this is that I expect a larger effect of the Range-hypothesis for the two-dimensional case; the number of targets for a dispersal scales with the squared range, instead of scaling linearly as in a one-dimensional space.

Using the suggested model, one must be careful when setting the parameters. It might be parameters for which fluctuations frequently cause clonal islands. In such a case the outcome is hard to predict, since the advantage of sexual reproduction can be negligible in clonal regions regardless of sex. I think the best way to set parameters is to let the dispersal ranges be small (so that a difference has a large impact), but still large enough to imply uniform distribution of the sexes.

4.4.2   Distribution of sexes in sexual offspring

In fully sexual species, the investments in female and male sexual offspring are usually equal, since it is the only stable steady state [13]. There are special circumstances when this is not the case, typically when inbreeding is expected due to low mixing of individuals [II]. Generally, however, the investments are equal. Thus, if males and females are of the same cost, they will be of the same frequency (as in humans). If the cost of a male is a tenth of the cost of a female, the sex ratio reflects this in that there are ten males on one female. The stability of equal investments in female and male offspring comes from the fact that a sexually produced offspring has exactly one mother and one father, and thus it is on average advantageous to have offspring of the minority sex.

In the models used for this thesis, a sexually produced offspring is assigned to be a female or a male with equal probabilities. This is the reasonable default assumption, but the necessity of this distribution is not straightforward, since reproduction is also asexual. I think that an investigation of the optimal strategy in a population with both reproduction types, could be of general interest. To my knowledge, this is not already an explored field.

I think that such an investigation could be done mathematically; assign a gene to every individual in the well-mixed model used for this thesis, let the gene affect the probability for female/male sexual offspring, and see whether this gene is expected to gain or loose ground. The analytical result

can then be verified by modeling the population. In Appendix F, I argue that, indeed, the evolutionary stable strategy is that there are equally many females as males in the sexual offspring. I call for critical examination of this argument, since I myself am not fully convinced of it. However, I can not see where the argument flaws.

4.4.3 Long-range dispersals

As argued in Section 4.2, the patterns observed for *F. radicans* can be caused by dispersals of longer range than what was modeled in the spatially explicit model. Therefore, I suggest the exploration of long-range dispersals. As Kleinhans et. al. found, clones can gain dominance through long-range relocations of adult individuals [12]. The effect of long-range relocations demonstrated in this study must be closely related to long-range dispersals of adventitious branches in our spatially explicit model.

When exploring the effects of long-range dispersals one must consider that they can be of different types. The local introduction of a new genotype and of the missing sex can be through dispersal of sperms, adventitious branches, zygotes or through hybridization with the sister species *F. vesiculosus*. To compare the outcome of these different types of long-range dispersals is of high interest.

Long-range effects (dispersals or hybridization with *F. vesiculosus*) have the potential to initiate the local processes explored with the models used in this thesis. Thus, the combination of insight into the local dynamics and the dynamics over larger distances can provide a general picture of processes in populations with mixed sexual and asexual reproduction. This is of particular interest when explaining patterns observed for *F. radicans* populations.

Appendices

A | Well-mixed model obtained in spatially explicit model

As will be shown in this appendix, the well-mixed model is obtained in the spatially explicit model when $\sigma = 0$ (no dispersals) and when $\sigma \to \infty$ (infinite dispersal range).

No dispersals

When $\sigma = 0$, there is no communication between different cells; no dispersed elements (sperms, adventitious branches or zygotes) leaved their producers, and no dispersed elements disperse into a cell from another cell. Thus we can consider the dynamics of an independent cell.

In a cell with $N_{m,\tau}$ males in generation τ, $sN_{m,\tau}$ sperms are dispersed. The number of zygotes produced is binomially distributed:

$$N_{zygotes,\tau} \sim \text{Bin}(sN_{m,\tau}, N_{f,\tau}/K) \tag{A.1}$$

An average, the number of zygotes produced is thus

$$\overline{N}_{zygotes,\tau} = s \frac{N_{f,\tau} N_{m,\tau}}{K}. \tag{A.2}$$

The clones produced is straightforward; $c_f N_{f,\tau}$ and $c_m N_{m,\tau}$. If s, c_f and c_m are large compared to K, we know that: 1) Within a short time the cell will be fully populated and 2) The probability of descendance is the same as in the well-mixed model. Thus, the spatially explicit model consists of

M independent well-mixed models with population size K if $\sigma = 0$ and s, c_f and c_m are large compared to K.

Infinite dispersal range

When $\sigma \to \infty$, there is no locality in the population; every dispersed element has the same chance to land in every cell. Thus we can consider the whole population.

If there are totally $N_{m,\tau}$ males in all cells in generation τ, then $sN_{m,\tau}$ sperms are dispersed. The dispersed sperms can land on any individual, and thus the number of zygotes is on average

$$\overline{N}_{zygotes,\tau} = s\frac{N_{f,\tau}N_{m,\tau}}{MK}. \tag{A.3}$$

The clones number of clones produced is given by $c_f N_{f,\tau}$ and $c_m N_{m,\tau}$. $N_{f,\tau}$ and $N_{m,\tau}$ scales linearly with M, and thus, if s, c_f and c_m are large compared to K, we know that: 1) Within short time all the cells will be fully populated and 2) When the cells are populated, the probability of descendance is the same as in the well-mixed model. Thus, the spatially explicit model approaches a well-mixed model with population size MK when $\sigma \to \infty$ and s, c_f and c_m are large compared to K.

B | Mathematical analysis of the the well-mixed model

Updating of sex ratio

The individuals that compete for entering generation $\tau + 1$ is:

$$c_f N_{f,\tau} + \frac{1}{2}s\frac{N_{f,\tau}N_{m,\tau}}{N} \quad \text{females}$$

$$\text{and} \tag{B.1}$$

$$c_m N_{m,\tau} + \frac{1}{2}s\frac{N_{f,\tau}N_{m,\tau}}{N} \quad \text{males.}$$

The number of individuals that compete is much larger than the ones that survives. Thus, the probability of an individual in generation $\tau + 1$ to be female is given by

$$p_{f,\tau+1} = \frac{c_f N_{f,\tau} + \frac{1}{2}s\frac{N_{f,\tau}N_{m,\tau}}{N}}{c_f N_{f,\tau} + c_m N_{m,\tau} + s\frac{N_{f,\tau}N_{m,\tau}}{N}}. \tag{B.2}$$

$N_{f,\tau} = Nx_{f,\tau}$ and $N_{m,\tau} = N(1 - x_{f,\tau})$, and thus

$$p_{f,\tau+1} = \frac{c_f x_{f,\tau} + \frac{1}{2}sx_{f,\tau}(1 - x_{f,\tau})}{c_f x_{f,\tau} + c_m(1 - x_{f,\tau}) + sx_f(1 - x_{f,\tau})}. \tag{B.3}$$

The expected number of females in generation $\tau + 1$ is $Np_{f,\tau+1}$, and the expected frequency of females equals $p_{f,\tau+1}$.

Independent parameters

Since the (large) number of competing offspring is

$$c_f N_{f,\tau} + c_m N_{m,\tau} + s\frac{N_{f,\tau}N_{m,\tau}}{N}, \tag{B.4}$$

and any group of offspring scales either with s, c_f or c_m, we must conclude that the three parameters are dependent and that there are exactly two independent parameters. For instance, the number of sexually born offspring from a subgroup of F_τ females and M_τ males scales with s, and the probability of an individual to be sexually produced from this subgroup only is

$$
\frac{s\frac{F_\tau M_\tau}{N}}{c_f N_{f,\tau} + c_m N_{m,\tau} + s\frac{N_{f,\tau} N_{m,\tau}}{N}}
$$
$$
= \frac{\frac{F_\tau M_\tau}{N}}{\frac{c_f}{s} N_{f,\tau} + \frac{c_m}{s} N_{m,\tau} + \frac{N_{f,\tau} N_{m,\tau}}{N}}.
\tag{B.5}
$$

This group of offspring scaled with s, and by dividing the probability with s, we see that the dynamics depend on the two parameters c_f/s and c_m/s. Since every term in an expression for a probability of descendance depends on only one of s, c_f or c_m, one re-write this expression in c_f/s and c_m/s by dividing with s.

Steady states of the sex ratio

The expected frequency of females in generation $\tau + 1$ is given by

$$
x_{f,\tau+1} = \frac{\frac{c_f}{s}x_{f,\tau} + \frac{1}{2}x_{f,\tau}(1 - x_{f,\tau})}{\frac{c_f}{s}x_{f,\tau} + \frac{c_m}{s}(1 - x_{f,\tau}) + x_f(1 - x_{f,\tau})}.
\tag{B.6}
$$

The expected change in female frequency is thus given by

$$
\begin{aligned}
\Delta x_{f,\tau+1} &\equiv x_{f,\tau+1} - x_{f,\tau} \\
&= \frac{\frac{c_f}{s}x_{f,\tau} + \frac{1}{2}x_{f,\tau}(1 - x_{f,\tau})}{\frac{c_f}{s}x_{f,\tau} + \frac{c_m}{s}(1 - x_{f,\tau}) + x_f(1 - x_{f,\tau})} - x_{f,\tau} \\
&= \frac{\frac{c_f}{s}x_{f,\tau} + \frac{1}{2}x_{f,\tau}(1 - x_{f,\tau}) - \frac{c_f}{s}x_{f,\tau}^2 - \frac{c_m}{s}x_{f,\tau}(1 - x_{f,\tau}) - x_{f,\tau}^2(1 - x_{f,\tau})}{\frac{c_f}{s}x_{f,\tau} + \frac{c_m}{s}(1 - x_{f,\tau}) + x_f(1 - x_{f,\tau})} \\
&= \frac{x_{f,\tau}(1 - x_{f,\tau})\left(\frac{c_f}{s} - \frac{c_m}{s} + \frac{1}{2} - x_{f,\tau}\right)}{\frac{c_f}{s}x_{f,\tau} + \frac{c_m}{s}(1 - x_{f,\tau}) + x_f(1 - x_{f,\tau})}.
\end{aligned}
\tag{B.7}
$$

We can conclude that there are three steady states:

- $x_f^* = 0$

- $x_f^* = 1$

- $x_f^* = \frac{1}{2} + \frac{c_f}{s} - \frac{c_m}{s}$

Since $x_{f,\tau}$ is $\in [0,1]$, the third case reduces to one of the other if $\left| \frac{c_f}{s} - \frac{c_m}{s} \right| \geq \frac{1}{2}$. However, if $\left| \frac{c_f}{s} - \frac{c_m}{s} \right| < \frac{1}{2}$, then all three steady states exists. We shall now investigate their stability.

If $\frac{c_f}{s} - \frac{c_m}{s} \geq \frac{1}{2}$, we have:

$x_{f,\tau}$	$\Delta x_{f,\tau+1}$	Steady state
0	0	Unstable
$\vdots$	+	-
1	0	Stable

If $\left| \frac{c_f}{s} - \frac{c_m}{s} \right| < \frac{1}{2}$, we have:

$x_{f,\tau}$	$\Delta x_{f,\tau+1}$	Steady state
0	0	Unstable
$\vdots$	+	-
$\frac{1}{2} + \frac{c_f}{s} - \frac{c_m}{s}$	0	Stable
$\vdots$	-	-
1	0	Unstable

If $\frac{c_m}{s} - \frac{c_f}{s} \geq \frac{1}{2}$, we have:

$x_{f,\tau}$	$\Delta x_{f,\tau+1}$	Steady state
0	0	Stable
$\vdots$	-	-
1	0	Unstable

C | Average time to loss of a sex in a fully sexual population

For a fully sexual population, the average time to lose one of the sexes is straightforward to calculate. Let us consider a scenario where the population size is N, all individuals are sexually produced, and a sexually produced individual is assigned to be female or male with equal probabilities. Then, given that a sex was not lost previously, it is lost with the probability

$$q = 2\left(\frac{1}{2}\right)^N = \left(\frac{1}{2}\right)^{N-1}. \tag{C.1}$$

Considering that the loss might have happened previously, the probability to lose the sex in generation τ is

$$p_\tau = (1-q)^{\tau-1}q. \tag{C.2}$$

Thus, the average time to loss is given by

$$T_{\text{loss}} = \sum_{\tau=1}^{\infty} \tau(1-q)^{\tau-1}q = \frac{1}{q}, \tag{C.3}$$

Inserting Equation (C.1) gives

$$T_{\text{loss}} = 2^{N-1}. \tag{C.4}$$

D | Speed of the sexual wave

Under these assumptions

- Zygotes does not disperse around their mother.

- Clonal birth rates are equal for females and males; $c_f = c_m \equiv c$.

- Sexual reproduction is much less frequent than clonal; $s/c \ll 1$.

- $K \gg 1$ (deterministic dynamics).

the speed of the sexual wave can be calculated to

$$v_s = \sigma\sqrt{\frac{s}{c}}. \tag{D.1}$$

Proof

If we consider a habitat of infinite size ($M \to \infty$), the cell index i can be replaced by a continuous space coordinate x. Then, the frequency of males at position x in generation $\tau + 1$ is given by

$$
p_{\tau+1}(x) = \frac{c \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)p_\tau(y) + \frac{1}{2}s \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)p_\tau(y)(1 - p_\tau(x))}{c + s \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)p_\tau(y)(1 - p_\tau(x))}
$$

$$
= \frac{\left(c + \frac{1}{2}s(1 - p_\tau(x))\right) \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)p_\tau(y)}{c + s(1 - p_\tau(x)) \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)p_\tau(y)}, \tag{D.2}
$$

where $f(x)$ is the probability density function for a normal distribution with standard deviation σ;

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{x^2}{2\sigma^2}}. \tag{D.3}$$

Now, we want to determine the integral $\int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) p_\tau(y)$. We can expand $p_\tau(y)$ around x, and obtain

$$p_\tau(y) \approx p_\tau(x) + \frac{\partial p_\tau(x)}{\partial x}(y-x) + \frac{1}{2}\frac{\partial^2 p_\tau(x)}{\partial x^2}(y-x)^2. \qquad \text{(D.4)}$$

Equation (D.4) is considered as an equality if $|x-y|$ is small. We can do this since the expression $f(x-y)$ occurs in the integral, and is negligeable for large $|x-y|$. Thus we have

$$
\begin{aligned}
\int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) p_\tau(y) = & \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) p_\tau(x) \\
& + \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) \frac{\partial p_\tau(x)}{\partial x}(y-x) \\
& + \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) \frac{1}{2}\frac{\partial^2 p_\tau(x)}{\partial x^2}(y-x)^2
\end{aligned}
$$

$$\text{(D.5)}$$

$$
\begin{aligned}
= & \; p_\tau(x) \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) \\
& + \frac{\partial p_\tau(x)}{\partial x} \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)(y-x) \\
& + \frac{1}{2}\frac{\partial^2 p_\tau(x)}{\partial x^2} \int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y)(y-x)^2.
\end{aligned}
$$

Replacing y with $t+x$, one obtains

$$
\begin{aligned}
\int\limits_{-\infty}^{\infty} \mathrm{d}y f(x-y) p_\tau(y) = & \; p_\tau(x) \int\limits_{-\infty}^{\infty} \mathrm{d}t f(t) \\
& - \frac{\partial p_\tau(x)}{\partial x} \int\limits_{-\infty}^{\infty} \mathrm{d}t f(t) t \\
& + \frac{1}{2}\frac{\partial^2 p_\tau(x)}{\partial x^2} \int\limits_{-\infty}^{\infty} \mathrm{d}t f(t) t^2
\end{aligned}
$$

$$\text{(D.6)}$$

.

The first term on the right hand side equals $p_\tau(x)$. Due to symmetry, the second term cancelles out. For the third term we have

$$\int_{-\infty}^{\infty} \mathrm{d}t f(t) t^2 = \int_{-\infty}^{\infty} \mathrm{d}t \frac{t^2}{\sigma\sqrt{2\pi}} e^{-\frac{t^2}{2\sigma^2}} = \sigma^2. \tag{D.7}$$

We have now arrived to

$$\int_{-\infty}^{\infty} \mathrm{d}y f(x-y) p_\tau(y) = p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}. \tag{D.8}$$

Inserting this into Equation (D.2) gives

$$p_{\tau+1}(x) = \frac{\left(c + \frac{1}{2}s(1 - p_\tau(x))\right)\left(p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}\right)}{c + s(1 - p_\tau(x))\left(p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}\right)}$$

$$= \left(p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}\right) \frac{\left(1 + \frac{s}{2c}(1 - p_\tau(x))\right)}{1 + \frac{s}{c}(1 - p_\tau(x))\left(p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}\right)}. \tag{D.9}$$

If we neglect the terms of order $s\sigma^2/c$ in the denominator, we obtain

$$p_{\tau+1}(x) = \left(p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}\right) \frac{\left(1 + \frac{s}{2c}(1 - p_\tau(x))\right)}{1 + \frac{s}{c}(1 - p_\tau(x))p_\tau(x)}. \tag{D.10}$$

By expanding this expression in terms of s/c and neglecting $\mathrm{O}\left(\left(\frac{s}{c}\right)^2\right)$, we arrive to

$$p_{\tau+1}(x) = \left(p_\tau(x) + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}\right)\left(1 + \frac{s}{2c}(1 - p_\tau(x))(1 - 2p_\tau(x))\right). \tag{D.11}$$

Once again neglecting terms of order $s\sigma^2/c$ gives

$$p_{\tau+1}(x) = p_\tau(x) + \frac{s}{2c} p_\tau(x)[1 - p_\tau(x)][1 - 2p_\tau(x)] + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}. \tag{D.12}$$

We define $\Delta p_{\tau+1}(x) \equiv p_{\tau+1}(x) - p_\tau(x)$, and re-write:

$$\Delta p_{\tau+1}(x) = \frac{s}{2c} p_\tau(x)[1 - p_\tau(x)][1 - 2p_\tau(x)] + \frac{1}{2}\sigma^2 \frac{\partial^2 p_\tau(x)}{\partial x^2}$$

$$\Rightarrow \frac{\Delta p_{\tau+1}(x)}{\frac{s}{2c}} = p_\tau(x)[1 - p_\tau(x)][1 - 2p_\tau(x)] + \sigma^2 \frac{c}{s} \frac{\partial^2 p_\tau(x)}{\partial x^2}. \tag{D.13}$$

Since $s/2c \ll 1$ we can define a continuous time t so that a time unit equals $s/2c$. Then we obtain

$$\frac{\partial p(x,t)}{\partial t} = p_\tau(x)[1 - p_\tau(x)][1 - 2p_\tau(x)] + \sigma^2 \frac{c}{s} \frac{\partial^2 p_\tau(x)}{\partial x^2}. \qquad \text{(D.14)}$$

This is a reaction-diffusion equation with

- Diffusion constant: $D = \sigma^2 \frac{c}{s}$

- Reaction term: $p_\tau(x)[1 - p_\tau(x)][1 - 2p_\tau(x)]$

Steady states are are obtained for $D = 0$; $p_1^* = 0$, $p_2^* = 1$ and $p_3^* = \frac{1}{2}$. The first two are unstable, the third is stable. We now want to asses whether the system allows for a traveling wave solution, connecting an unstable state with a stable. In order to answer this question we assume that:

- $z = x - vt$

- $p(x,t) = u(x - vt) = u(z)$,

where v is the speed of the wave.

We now find that

$$\frac{\partial p(x,t)}{\partial t} = \frac{\partial u(z)}{\partial z} \frac{\partial z}{\partial t} = -v \frac{\partial u(z)}{\partial z}, \qquad \text{(D.15)}$$

and

$$\begin{aligned}
\frac{\partial^2 p(x,t)}{\partial x^2} &= \frac{\partial}{\partial x}\left(\frac{\partial p(x,t)}{\partial x}\right) = \frac{\partial}{\partial x}\left(\frac{\partial u(z)}{\partial x}\right) \\
&= \frac{\partial}{\partial x}\left(\frac{\partial u(z)}{\partial z}\frac{\partial z}{\partial x}\right) = \frac{\partial}{\partial x}\left(\frac{\partial u(z)}{\partial z}\right) \\
&= \frac{\partial}{\partial z}\left(\frac{\partial u(z)}{\partial x}\right) = \frac{\partial}{\partial z}\left(\frac{\partial u(z)}{\partial z}\frac{\partial z}{\partial x}\right) \\
&= \frac{\partial}{\partial z}\left(\frac{\partial u(z)}{\partial z}\right) = \frac{\partial^2 u(z)}{\partial z^2}.
\end{aligned} \qquad \text{(D.16)}$$

The boundary conditions are

- $u(\infty) = 0$ or $u(\infty) = 1$

- $u(-\infty) = \frac{1}{2}$

Equation (D.14) can now be expressed as

$$D\frac{\partial^2 u}{\partial z^2} + u(1-u)(1-2u) + v\frac{\partial u}{\partial z} = 0. \tag{D.17}$$

If we introduce $w \equiv \frac{\partial u}{\partial z}$, this is transformed to the two equations

$$\begin{aligned}\frac{\partial u}{\partial z} &= w \\ \frac{\partial w}{\partial z} &= -\frac{1}{D}u(1-u)(1-2u) - \frac{v}{D}w.\end{aligned} \tag{D.18}$$

The Jacobian for this system is

$$\mathbf{J} = \begin{bmatrix} 0 & 1 \\ -\frac{1}{D}(1-6u+6u^2) & -\frac{v}{D} \end{bmatrix}, \tag{D.19}$$

and the eigenvalues are found by solving

$$\lambda\left(\frac{v}{D} + \lambda\right) + \frac{1}{D}(1-6u+6u^2) = 0. \tag{D.20}$$

For the stable states $(u^*,w^*)_1 = (0,0)$ and $(u^*,w^*)_2 = (1,0)$, we find that

$$\lambda_{1,2}^{(1),(2)} = -\frac{v}{2D} \pm \frac{1}{2}\sqrt{\frac{v^2}{D^2} - \frac{4}{D}}. \tag{D.21}$$

Thus, these are stable nodes (or stars) if $v \geq 2\sqrt{D}$ or stable spirals if $v < 2\sqrt{D}$.

For the stable state $(u^*,w^*)_3 = (1/2,0)$, we find that

$$\lambda_{1,2}^{(3)} = -\frac{v}{2D} \pm \frac{1}{2}\sqrt{\frac{v^2}{D^2} + \frac{2}{D}}. \tag{D.22}$$

Both eigenvalues are real and with opposite signs, and thus this is a saddle point.

Since u is $\in [0,1]$, spirals are not physical solutions to the system. Thus, only $v \geq 2\sqrt{D}$ renders solutions that are physically meaningful. If $v \geq 2\sqrt{D}$, there exists a trajectory that connects the stable steady state with the unstable. We must conclude that there is a traveling wave solution to the system, and that the minimum speed of the wave is $v = 2\sqrt{D}$, where $D = \sigma^2\frac{c}{s}$. Recall that the introduced the continuous time $t = \tau\frac{s}{2c}$. Thus, in the ordinary time step, we obtain

$$v_s = \frac{\partial x}{\partial \tau} = \frac{\partial x}{\partial t}\frac{\partial t}{\partial \tau} = 2\sigma\sqrt{\frac{c}{s}}\frac{s}{2c} = \sigma\sqrt{\frac{s}{c}}. \tag{D.23}$$

Verification

In Figure D.1 the parameters are:

- $K = 1000$

- $s = 10$

- $c_f = c_m = 200$

- $\sigma = 0.5$

This gives the speed of the sexual wave: $v_s = \frac{1}{4\sqrt{5}} \approx 0.112$ cells per generation. We can see that this estimates the actual speed in our spatially explicit model well, even though the assumption of no zygote dispersal was violated. Especially, the estimation is good for the speed of the sexual wave into female clonal regions. This is due to that, above, if was this specific wave speed that was derived.
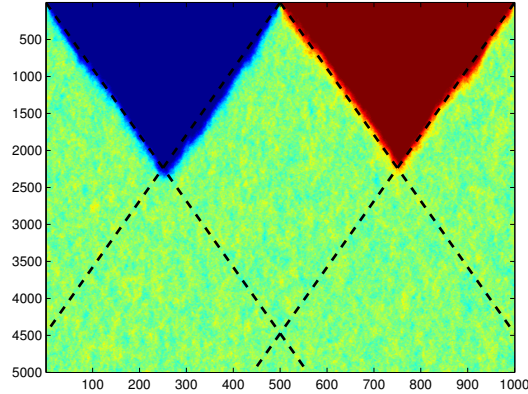

Figure D.1: Verification of the speed of the sexual wave. Dashed black lines are the theoretically predicted wave front. The initialization was "Male and female colony". For color notation and initialization, see the beginning of Section 3.2.

E | Model that could verify the Range-hypothesis

This is the algorithm of a model that could verify the Range-hypothesis:

- Individuals are distributed over a two dimensional array of cells, where each cell contains one individual. Individuals are either male or female.

- Each individual i has two genes; $F_i \in [0,1]$ and $M_i \in [0,1]$.

- In every generation, an individual invests 1 resource unit in reproduction.

  - If the individual is a female she invests F_i resource units in sexual reproduction and $1 - F_i$ resource units in asexual reproduction.
  - If the individual is a male he invests M_i resource units in sexual reproduction and $1 - M_i$ resource units in asexual reproduction.

- The investments of an individual are dispersed in its vicinity.

  - The sexual investments of a female are uniformly distributed over all cells that are within a distance $\leq \sigma_e$ from her.
  - The sexual investments of a male are uniformly distributed over all cells that are within a distance $\leq \sigma_s$ from him.
  - The asexual investments of any individual are uniformly distributed over all cells that are within a distance $\leq \sigma_c$.

- After all dispersals, the amount of offspring in each cell is determined.

  - The amount of female clonal offspring in a cell equals the total amount of resource units spent on asexual reproduction that females dispersed to it.
  - The amount of male clonal offspring in a cell equals the total amount of resource units spent on asexual reproduction that males dispersed to it.
  - If the total amount of resource units spent on sexual reproduction in females in a cell is f, the total amount of resource units spent on sexual reproduction in males in a cell is m, then the amount of sexually produced offspring in that cell is sfm. Here,

$s > 0$, is a parameter that can adjust for the relative advantage/disadvantage of sexual reproduction in relation to asexual.

- All offspring compete neutrally to enter the next generation. The individual that wins in a cell is assigned to be a female clone, a male clone or a sexually produced offspring with probabilities proportional to their amounts of offspring.

  - If a female clone wins, its genome is a copy of a female that contributed with asexual investments to the cell. The specific parent is a female that is picked with a probability that is proportional to her contribution of clonal offspring.

  - If a male clone wins, its genome is a copy of a male that contributed with asexual investments to the cell. The specific parent is a male that is picked with a probability that is proportional to his contribution of clonal offspring.

  - If a sexually produced offspring wins, its mother is a female that contributed with sexual investments to the cell. The specific mother is a female that is picked with a probability that is proportional to her contribution of sexual investments. The father is a male that contributed with sexual investments to the cell. The specific father is a male that is picked with a probability that is proportional to his contribution of sexual investments. After the mother and father is determined, the individual inherits its genome from them:

    * With the probability $\frac{1}{2}$ the sexually produced offspring inherits its M-gene from its mother, otherwise the gene is inherited from the father.
    * With the probability $\frac{1}{2}$ the sexually produced offspring inherits its F-gene from its mother, otherwise the gene is inherited from the father.

  The sexually produced offspring is assigned to be a female or a male with equal probabilities.

- In the new generation, every gene is mutated with the probability μ. If a gene is mutated it is set to a random number $\in [0,1]$.

F | Evolutionary stable strategy for distribution of sexes in sexual offspring

Consider the population in the well-mixed model described in Section 2.1. Here, a sexual offspring is assigned to be a female or a male with equal probabilities. But if the probability evolved - what would then be the outcome? In the following, I argue that, when the genome(s) of the mother and/or the father influences this probability, the distribution will remain 50-50. I myself am not completely convinced by my argument, but I can not see where it flaws. Therefore, I welcome critical review.

Motivation

Let us assume that each individual has a genome that codes for a "preferred probability" of a sexually born offspring to be female. We now consider a sexually produced offspring with mother i and father j. Here, we denote the probability that this offspring is female with $p_{i,j}$. Also, we denote the preferred probability for the mother p_i, and the preferred probability of the father p_j.

Furthermore, we assume that the probability of the sexually born offspring to be female is either up to the mothers or up to the fathers preference, or that the probability is a compromise of the two preferences, in that

$$p_{i,j} \in [\min(p_i, p_j), \max(p_i, p_j)]. \tag{F.1}$$

The parents of a sexually produced offspring is a randomly picked female-male pair. Thus, the probability of a sexually produced offspring to be female is

$$P = \frac{1}{N_f N_m} \sum_{i=1}^{N_f} \sum_{j=1}^{N_m} p_{i,j}. \tag{F.2}$$

From this, one can conclude (analogous to as in Appendix B) that

$$N_f^* = N \left(P + \frac{c_f - c_m}{s} \right) \tag{F.3}$$

is the only non-trivial stable steady state of the sex ratio if and only if

$$c_m - c_f < sP \quad \text{and} \quad c_f - c_m < s(1-P). \tag{F.4}$$

Let us assume that we are in such a non-trivial steady state. Since clonal offspring inherits the full genome and sexual offspring inherits half the genome, the amount of competing genome per female is proportional to

$$
\begin{aligned}
c_f + \frac{1}{2}s\frac{N_m^*}{N} \\
= c_f + \frac{1}{2}s\frac{N - N_f^*}{N} \\
= c_f + \frac{1}{2}s\left(1 - P - \frac{c_f - c_m}{s}\right)
\end{aligned}
\tag{F.5}
$$

, and the amount of competing genome per male is

$$
\begin{aligned}
c_m + \frac{1}{2}s\frac{N_f^*}{N} \\
= c_m + \frac{1}{2}s\left(P + \frac{c_f - c_m}{s}\right).
\end{aligned}
\tag{F.6}
$$

Thus, a gene will compete with the same number of copies in a female and a male if and only if

$$
\begin{aligned}
c_f + \frac{1}{2}s\left(1 - P - \frac{c_f - c_m}{s}\right) &= c_m + \frac{1}{2}s\left(P + \frac{c_f - c_m}{s}\right) \\
\Rightarrow 2c_f + s - sP - c_f + c_m &= 2c_m + sP + c_f - c_m \\
\Rightarrow 2sP &= s \\
\Rightarrow P &= \frac{1}{2}.
\end{aligned}
\tag{F.7}
$$

Now, if $P > \frac{1}{2}$, males spread genes more that females. All genes that code for a preferred probability $< P$ will be more successful than all genes that code for a preferred probability $\geq P$. Thus P will decline with time. If, on the other hand, $P < \frac{1}{2}$, females spread more genes than males. Now all genes that code for a preferred probability $> P$ will be more successful than all genes that code for a preferred probability $\leq P$, and P will increase with time. Thus

$$
\begin{aligned}
\frac{\mathrm{d}P}{\mathrm{d}t} &< 0 \quad \text{if} \quad P > \frac{1}{2} \\
\frac{\mathrm{d}P}{\mathrm{d}t} &> 0 \quad \text{if} \quad P < \frac{1}{2}
\end{aligned}
\tag{F.8}
$$

, and we must conclude that $P = \frac{1}{2}$ is a stable steady state; within time, we will have a probability that a sexually born offspring is female given by

$$P^* = \frac{1}{2}. \tag{F.9}$$

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