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Mathematical models for the coexistence of sexual and asexual conspecifics

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Mathematical Models for the Coexistence of Sexual and Asexual Conspecifics

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Abstract

Eukaryotic sexual reproduction involves meiosis and outcrossing, processes by which haploid, genetically non-uniform nuclei fuse to produce the nucleus of a zygote. Thus, sexually reproducing organisms pass only half of their genes to their offspring. Asexual reproduction, on the other hand, may imply the full replication of the maternal genotype. There is an obvious two-fold cost of sex in the face of asexual reproduction. In the event that asexual reproduction evolved from sexual reproduction — after a mutation, for example — it would be expected to quickly displace its predecessor. However, sex remains the most common reproductive strategy. Moreover, sexual and asexual forms of the same species coexist, even in those cases where the latter are clearly descended from their sexual counterparts. These observations constitute what has been called the queen of evolutionary questions: why the evolution and maintenance of sex. This problem has attracted the attention of biologists and mathematicians alike. Traditional mathematical models have repeatedly shown that in a population where both forms of reproduction are present only one can prevail. Yet, the coexistence of sexual and asexual relatives is common in nature. Thus, mathematical models have failed to reflect the real world in this case (the exception being those where external agents, such as parasites, are invoked). In this thesis, a revision of the ways in which this problem has been modelled is advocated for. Namely, the introduction of some spatial aspects of the ecology of mixed populations will be given vast consideration. This work is a collection of mainly spatial models, within the context of populations of hermaphrodite flowering plants, that explore the coexistence of sexual and asexual conspecifics.

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A la UNAM

Contents

It is obvious that this essay can only contain an attempt at an explanation, an hypothesis, and not a solution which is above criticism, like the results of mathematical calculation. But no biological theory of the present day can escape a similar fate, for the mathematical key which opens the door leading to the secrets of life has not yet been found...

August Weissman, 1887.

Introduction

The words 'asexual reproduction' conjure up a school lesson when we all learnt that a cell may split into two identical copies of itself, or the image of a person in a garden, cutting parts off a plant, putting them in pots and obtaining 'new' plants from them. If asked why sex exists at all and what sexual reproduction is, we may wonder where the person asking these questions has been living. Is it not obvious that sex is the pairing of two beings of different genders — even if they are bacteria, surely there are male and female bacteria — with the purpose of producing new beings? In short, is not the answer contained in the question?

When we give these questions consideration, we discover that sex and reproduction are not one and the same thing, that there are not necessarily two genders (*e.g.* fungi have tens of them; Fincham *et al.*, 1979) or separate packages for each of them if one thinks of hermaphrodites. We also discover that plants grown from cuttings are not an example of reproduction and that an amoeba splitting in two is not the only instance of asexual reproduction. When we actually understand what reproduction means and learn to distinguish its sexual from its asexual variants — not a trivial task, let it be said — we will still be surprised by the fact that sex persists given that asexual reproduction seems more efficient and less costly. Moreover, it has been observed to coexist with asexual reproduction.

These considerations are just the amateur version of a debate that evolutionary biologists have had across three centuries now. In 1862, Charles Darwin was the first to pose the questions 'why sex?', 'why sexes?' Answers have been put forward since the late 19th century, but theories are just now, in the late 20th and early 21st centuries, being put together, and not all the scientists involved can agree on all of them. We say scientists because it is not only evolutionary biologists who have been concerned with the evolution and maintenance of sex, neither with the coexistence of sexual and asexual forms, but also mathematicians and physicists and, most probably, (natural) philosophers.

Mathematics has a relationship with Biology that matures as its acceptance, that is, the realisation that numbers help in describing the natural world, grows among biologists. The scenario has changed from the very first crude models developed by Malthus to describe population growth and use of resources, in the 18th century. Numbers *per se* are not the ultimate word. Concern now revolves around the importance of creating a real link between these disciplines, one that provides biologists with models that are close to what they observe in the laboratory or in the field. In this context, one aspect has taken centre stage: space (Tilman and Kareiva, 1997, and Neuhauser, 2001, offer relevant discussions about this centre role of space in ecological modelling). The real world is spatial. Traditional mathematical models did not take space into account. It is not surprising that, insightful as many have been, they often failed to accurately describe natural phenomena. To illustrate how considering space may change the conclusions drawn after observation of a biological system, let us recall Gause's experiments with *Paramecium caudatum* and *P. bursaria*. These protozoans were observed to coexist despite being competitors. This seemed to contradict the Principle of Competitive Exclusion, which states that in a competitive system the strongest competitor will exclude the weaker ones. Upon closer examination, it was noticed that these species were not coexisting but living in different regions of the liquid medium where they were cultivated. *P. caudatum* tended to live and feed on the bacteria suspended in the medium, while *P. bursaria* thrived on the yeast cells at the bottom of culture. The Principle of Competitive Exclusion is now found in Ecology textbooks (*e.g.* Begon *et al.*) as follows: competitive species coexist only if they do not have the same demands on shared resources.

Concisely speaking, this thesis is about exploring the spatial modelling of the ecological aspects of the coexistence of sexual and asexual forms within a species. This work is inscribed in the context of mathematical biology. As such, first of all the biological situation under study will be presented, together with the aspects to be addressed by this piece of research. Care has been taken to make certain biological concepts clear, as the reading of the rest of the work will depend on this basic understanding. But other terms, perhaps less obvious or familiar, will seem to have been taken for granted. That is not the case. They will appear throughout the text in bold italic characters so that the reader may look them up in the glossary at the end of the thesis. This is similar to relegating detailed mathematical discussions or proofs to appendixes at the end of the chapter where they appear. In both cases the aim is to keep the text flowing and refer more interested readers to parts of the thesis that contain the relevant information.

Chapter 1 contains a description of the biological situation to be studied, together with an overview of previous treatments of the problem. It also establishes what the lines and aims of the research contained in this thesis are, and concludes by stating the modelling assumptions that will be made throughout the models presented. The reader will notice that these assumptions are included every time a model is presented. Although this could be considered too repetitive for the attentive reader, the reason for such redundancy is to make every chapter as self contained as possible. Was this not so, the reader would have to be returning to chapter 1, in addition to the references to appendixes and glossary that contain mathematics and biology in more detail.

Thus, after the biological terms, history and aims have been presented, the mathematical work in the thesis begins in chapter 2 with a traditional (mass-action law) model where space is not taken into account. This may seem out of place in a work whose chief goal is to explore spatial considerations, but it turns out to be of much help in making the growth dynamics of a population of hermaphrodite flowering plants of sexual and asexual relatives clear. Moreover, this model summarises most approaches that had been taken towards the sex *vs.* asexuality question until recently. The scope of the models in the thesis has been narrowed, from the broad topic in evolutionary biology described above, to this very representative example —flowering plants— because most asexual taxa of flowering plants are descended from hermaphrodite (sexual) ancestors. Species such as those in *Taraxacum* or *Towsendia* provide many good examples of natural populations where sexual and asexual forms coexist and also have distinctive geographical distributions.

Once the limitations of a temporal-dynamics-only model are discussed, from the 3rd chapter onwards, the thesis fully moves into the spatial modelling of a population mixed for reproductive mode. The first attempt is a patch-occupancy model where the introduction of space is implicit. Indeed, although the space is assumed to be a collection of patches inhabited by the species, nothing is included in the model as to where these patches are or what distances separate them. Mathematically, one works with difference equations that describe how the proportions of patches in a given state (*e.g.* empty/occupied) change over time. The results, however, already show that the spatial paradigm has many new things to offer the researcher. A second model within this chapter, one that considers the interaction between sexual and asexual forms via the male function in asexuals, proves to be robust as the coexistence result, as well as the exclusion results, are still observed in the modified system.

Having created a patch-occupancy model, moving on to a cellular automaton in chapter 4 is, from the modeller's point of view, natural. The habitat is readily identified with a lattice of sites, the interaction between sexual and asexual individuals is translated into a set of transition rules and simulation in a computer is, barring programming limitations, straightforward. From the biological point of view, moreover, accuracy is also gained. In populations of flowering plants spatial interactions are extremely localised mainly because plants are sessile organisms. An individual effectively competes for resources with only those individuals in proximity to it. What this neighbourhood of effective interaction is has been the subject of another interesting discussion among biologists and geneticists. In the context of this thesis, the importance of the ecological neighbourhood is made evident when one considers that pollen dispersal by insects is highly localised. A cellular automaton can easily reflect this spatial limitation.

Another important spatial aspect of the ecology of plants is the dispersal of propagules. Being sessile, this is the stage in their life histories when they have the opportunity to move to new territory. How far their propagules disperse and what the consequences of dispersal are for the range and stability of the population are a source of interesting work for ecologists, geneticists and statisticians alike. Dispersal has been traditionally studied by means of reaction-diffusion models. Therefore the thesis retakes this approach in chapter 5. However, care is taken to provide a model that is closer to the biology of these populations by incorporating long-distance dispersal of propagules. Often neglected in models, propagules that reach further from the mean are an important way of population spread. Finally, chapter 6 moves on from its predecessor by realising that the patterns of dispersal implicit in a reaction-diffusion formalism do not accurately reflect long-range dispersal and may not be better approximated by the advection term used in chapter 5. Thus, it uses a very modern approach, integro-difference equations, to explore those models where this aspect may be effectively introduced.

Every chapter offers the reader a presentation of the mathematical technique chosen to model a given aspect of the ecology of the populations under study. Once the model has been presented and analysed, the results of each approach are discussed at the end of the corresponding chapter. This thesis concludes with a general discussion where all the different approaches are discussed and their results contrasted. It is the aim of this final section to show the reader if this work was of any contribution to a rich problem that has baffled, and very likely will continue to amaze, many observers and modellers of nature.

Chapter 1

The Biological Context

This chapter is about introducing the reader to the biological situation addressed by the models presented in this thesis. It will start by briefly introducing basic terminology. It will go on to give a historical overview of the treatments to the biological questions posed and will finally point the reader into the direction this piece of research takes.

1.1 A common language

The words reproduction, sexuality, asexuality, sexual or asexual individual(s), or sexual(s) and asexual(s) for short, will appear many times in this work. Biologists have sustained thoughtful discussions about the definition of fundamental concepts such as individual, population, reproduction and growth. They still cannot agree on what these definitions should be. The task is indeed so difficult that some 'specialised' dictionaries may omit as intrinsic a term to Biology as 'individual' (Hale *et al.*, 1995), while other works may devote entire paragraphs or pages to the same term (Mogie, 1992; Begon *et al.*, 1996). Although it is not pertinent here to enter into the realms of Philosophy of Science, it is important to lay some basic terminology at the very start of this work, so that throughout this text it is clear what is meant by individual, population, reproduction and, most importantly, sexual and asexual reproduction.

A basic biological function of every individual is to pass its genetic information on to the next generation, either through reproduction or, because relatives share genes in common, through kin-selected altruism (Hamilton, 1963, 1964; Maynard Smith, 1964). There, in one sentence 'individual' and 'reproduction' have already appeared. In the words of Mogie (1992):

"Reproduction is the event which initiates a recapitulation of ***on-***

> ***togeny*.** That is, reproduction re-sets ontogeny. ***Growth*** is the part of the process ... which causes ontogeny to progress from its earliest to its latest stages. The individual is the unit associated with a single ontogenetic progression."[1]

This is what the author concludes after a brief survey of the terms reproduction, growth and individual. It is also the view this work will adopt. What it means is that reproduction is an event that produces a new individual from a single cell that, through a process described as growth, initiates a lineage of cells that multiply, differentiate and develop into a new organism. Through growth, this new individual may even be separated into modules (clonal growth) rather than being an indivisible unit, but growth will not bring fundamental changes to the identity of the structure that was initiated at reproduction. An entity thus formed is what will be understood by the term individual.

Given that reproduction has such a central role in the life of an organism — some authors even claiming that it is the sole purpose of life and individuals are just the vehicles for genes to perpetuate themselves (Dawkins, 1976)— it is not surprising that so many strategies to achieve reproduction have evolved. Among all these, this work is concerned with making a clear distinction between those that imply the ***recombination*** of genetic material and those that do not: that is to say, sexual *vs.* asexual reproduction. Borrowing again from Mogie (1992):

> "...sexual reproduction involves the initiation of an individual from a single cell, which must be a ***zygote*** or a zygote equivalent, whose nucleus is formed by ***syngamy***... asexual reproduction [involves] the initiation of an individual from a single cell, which must be a zygote equivalent, whose nucleus is not formed by syngamy."[2]

At the core of this plain definition lies what is considered to be the main difference between sexual and asexual reproduction: the presence or absence, respectively, of the recombination of genetic material, the fusion of ***gametes*** or nuclei. First, consider the simplest and best known example of asexual reproduction: the production of two identical unicellular individuals from one parental cell after a ***mitotic division***. Each daughter cell inherits the full set of chromosomes of the mother cell[3]. Sexual reproduction in ***eukaryotes***, on the other hand, involves ***meiotic division*** of cells to produce gametes, recombination of

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[1] Mogie, M. (1992) *The Evolution of Asexual Reproduction in Plants*, p. 10.

[2] Mogie, M. *op. cit.*, p. 15.

[3] Barring ***mutations***.

genetic material during meiosis and fusion of pairs of gametes. Although it is not always true that asexual reproduction implies the faithful reproduction of the maternal genome[4], it is clear that sex produces offspring that are different from the parents.

A further biological unit referred to throughout this thesis is that of the population. This will be defined as:

> "... a group of individuals of one species in an area."[5]

Although this is by no means a universal definition, give and take some elements, most authors seem to agree on this term.

1.2 Of sex and queens

On the basis of the most accepted scientific theories on the origin of life (Oparin, 1953; Lazcano-Araujo, 1992), it seems reasonable to think that the first mode of reproduction must have been asexual and that sex could have evolved anytime between three and one billion years ago (Greenwood and Adams, 1987). Common sense suggests that the purpose of sex is the production of offspring. This obvious function of sex remained unquestioned until the late 19th century when Charles Darwin (1862) wrote:

> "We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of ***parthenogenesis***... The whole subject is as yet hidden in darkness."[6]

This was echoed three decades later by Weissman (1891):

> "But if amphimixis [sexual reproduction] is not absolutely necessary, the rarity of purely parthenogenetic reproduction shows that it must have a wide-spread and deep significance. Its benefits are not to be sought in the single individual; for organisms can arise by agamic [asexual] methods... hence we are led to enquire, *how nature can best have undertaken to give this amphimixis the widest possible range in the organic world.*"[7]

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[4] *E.g.* in ***haplo-diploid*** social insects males are initiated by the asexual development of an egg that is meiotically reduced and that therefore only contains half of the maternal genome.

[5] Begon *et al.* (1996) *Ecology,* p. 569.

[6] Barrett, P.H. (1977) *The Collected Papers Of Charles Darwin,* p.61. Darwin's original reference (1862) is also given in the bibliography.

[7] Weissman, A. (1892) *Essays upon Heredity and Kindred Biological Problems,* v. II, p. 199; his italics.

Following these comments, sex did not seem an obvious, functional or even sensible way of reproduction. For one thing, it is energetically demanding because it involves the various processes of meiosis, recombination and fusion of genetic material. Furthermore, it has physiological costs as it requires the production of specialised reproductive cells, gametes, and even different types of them or their carriers (***isogamy** vs. **anisogamy, dioecy** vs. **hermaphroditism***). For some species, sex is additionally associated with behavioural costs arising from all the paraphernalia, rituals and competition necessary to find a suitable mate (Greenwood and Adams, 1987). Compared to certain forms of asexual reproduction such as ***binary fission*** or parthenogenesis, sex does not look efficient at all. During the 1970s, two of the evolutionary biologists now most associated with studies of the evolution of sex, John Maynard Smith and G.C. Williams, put this in numbers: if a female gave up sexual reproduction and had only daughters descended from unfertilised eggs, she would immediately have twice as much genetic representation in the next generation. Sex has a two-fold disadvantage in terms of what is called the cost of males (Maynard Smith, 1971) or the cost of meiosis (Williams, 1975).[8] Since then, a matter that was considered solved became the centre of a debate that has lived into the 21st century. 'Why sex?' has been named the queen of evolutionary questions (Bell, 1982).

It must not be understood that the discussion of why sex is advantageous lay dormant until the 1970s. Weismann (1885) himself offered the first explanation:

> "I do not know what meaning can be attributed to sexual reproduction other than the creation of hereditary individual characters to form the material upon which natural selection may work."[9]

In Weismann's line of thought, evolution was a mandatory process in life and sex provided lineages with the ability to adapt and change as quickly as evolution required. But stabilising selection can slow or prevent evolutionary change. There are examples of species which have remained almost unchanged for millions of years (e.g. *Latimeria chalumnae,* the coelacanth, is very similar to its ancestors that existed more than 300 million years ago), while there are others whose evolution has been speeded up by man, for example in respect to environmental conditions such as pollution (*e.g.* some melanic forms of the moth *Biston*

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[8] With amazing prescience (1885), Weissman had stated the two-fold cost of sex when he wrote: "Such increased fertility might well be produced by pure parthenogenesis..., by means of which the number of egg-producing individuals in all the previous sexual generations would be doubled." He was at the time more concerned with the significance of sexual reproduction and did not pursue this observation. Weissman, A. (1889) *op. cit.*, v. I, p.290.

[9] Weismann, A. (1889) *op. cit.*, v. I, p. 281.

betularia) or artificial selection (*e.g.* dogs, horses and crop species). Once this fallacy had been exposed, influential works by Weismann's followers were the first attempts from the field of genetics to explain the advantages of sexual reproduction. Fully acknowledging that new genetic combinations are the product of a fortuitous rather than directed process, Fisher (1930, 1937) and Müller (1932) argued that sexual species could share those inventions while asexuals could not. This was considered enough to declare the problem of sex clarified. In 1965, Crow and Kimura produced a mathematical model that showed how mutations in different organisms can be brought together in sexual populations but not in asexual ones. Mathematics had thus sealed the argument.

The 1960s saw the origin of another discussion among evolutionary biologists. The issue at the centre of the new argument was to decide what the unit of selection was: the individual or the species. The language in which evolution had been written and discussed allowed the discussion to switch carelessly between the individual and the species. Even Charles Darwin's masterpiece, *The Origin of Species*, bore this confusion in its title, although the emphasis of the book is certainly on competition among individuals, not among species. But in 1962 a book was published by V.C. Wynne-Edwards in which he made a case for group selection. His studies about animal behaviour led him to believe that in certain species strategies are evolved so that the benefits are for the whole group and not just for an individual. His book divided evolutionary biologists into group and individual selectionists. The most important answer to the group-selectionist movement was another book, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, by G. C. Williams (1966). This apparently different discussion had important consequences for the theories of sex, as shall be seen later. Its repercussions prompted Maynard Smith and G.C. Williams to state the costs of sex and move the debate into the 1970s. The last thirty years have seen a wealth of scientific literary production trying to find an explanation for sex. It is accepted that sex must have enough evolutionary advantages to have overcome its two-fold costs and become established as the most common type of reproduction, but none of the proposed theories has received unanimous approval. All these theories can be roughly divided into those originating from molecular biology, genetics or ecology (Kondrashov, 1993).

The explanation for sex put forward by molecular biologists relies on the fact that the same mechanisms involved in gene repair are those involved in the recombination of genetic material. DNA is constantly damaged by UV radiation and chemicals. It is then repaired by enzymes, which get information on what the original strand was like from the complementary strand in the double helix molecule. But often both strands are damaged and information for repair can only be found in the copy of the same gene provided by another organism via sex. The probability that this second copy is damaged at the same place is very small. Harris Bernstein is the foremost advocate of this view (1977). He bases his argument that sex exists to repair genes on experiments with *E. Coli* and *Drosophila*, where it was noticed that mutant individuals who are unable to repair genes cannot recombine them either (Bernstein, 1983; Bernstein *et al.*, 1981, 1988). Further evidence that sustains the repair theory is the fact that organisms exposed to damaging UV rays react better when they are capable of recombination, and even better if they are ***diploid***. Mutations that interfere with recombination make their carriers particularly susceptible to ultraviolet light. The gene repair theory also explains why three quarters of the meiotic product are disposed of when gametes are produced. According to it, that is a mechanism which puts together all errors that are to be repaired (Bernstein, 1983; Bernstein *et al.*, 1985). Although it has been accepted that gene repair could be the reason for the origin of sex, scientists from other fields such as genetics or ecology doubt that this is the reason why sex has been maintained (West *et al.*, 1999; Rice, 2002; Otto and Lenormand, 2002).

Geneticists are concerned with mutations, which occur frequently. These changes in the genetic information of an organism cannot be repaired. Some of them may be beneficial and some harmful to their carriers, although only about one per percent of them have evident effects, the rest being described as 'silent' as they change the DNA but not the resulting information.[10] However low the mutation rate may be, it does produce a gradual and steady accumulation of genetic changes (Kondrashov, 1988). Thus, from the field of genetics there are theories concerning good and bad mutations.

Optimistic geneticists focused on mutations that brought improvement to the genetic make-up of organisms, — beneficial mutations. Agreeing with their predecessors, they also concluded that sex was the means to bring such fortunate inventions together. That is, without sex, each beneficial mutation would be restricted to the organism that obtained it or to its asexually produced descendants. Along the good-mutation line, Kirkpatrick and Jenkins (1989) looked at bene-

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[10] Mogie offers the following analogy: fertilisation and fertilization are two different spellings of the same word. Although one character has been changed, s to z or vice versa, the concept remains untouched and anybody will understand what is being meant, regardless of the spelling. Other changes of just one character, however, can completely change the meaning of what is being said. Consider changing 'i' in fit to 'a', to obtain fat. Silent mutations are the analogies of different spellings of the same word.

ficial but recessive mutations. In order to express themselves, these mutations would have to be 'invented' more than once in an asexual individual, a highly unlikely event, whereas the offspring of sexual individuals could get the necessary number of copies to fully express the new character. To these geneticists, another advantage of sex was that it could also reduce linkage disequilibria. That is, genes that are normally associated can be split during recombination and then outcrossed so that the resulting offspring no longer carry those genetic associations. Instead, the population acquires many new useful genetic combinations. But here precisely lies the counterargument to the 'good-mutation' explanations of sex: recombination does not necessarily bring together beneficial mutations. Sex creates new combinations, among which those fortuitous ones are, but it is more likely to break combinations, regardless of how beneficial or harmful they are. The trademark of sex is that it creates offspring that are different from whatever there was before. There is randomness in sex (Stearns, 1987; Michod and Levin, 1988).

It is now the turn of bad mutations. Müller was among the initiators of genetic explanations of sex and gave full form to one of them (Müller, 1964) that is today well known as Müller's ratchet. In a very simplified way, the argument is that harmful mutations gradually accumulate in a population. Only a few individuals are free of them. Sex is the way in which these 'pure' lines can be incorporated into the gene pool before their carriers die. The analogy with the ratchet is that the accumulation of genetic defects cannot be turned back, unless there is sex. That is, because an asexually reproduced organism inherits the entire parental genome (in most taxa), it cannot have fewer mutations than its parent. In contrast, because a sexually reproduced organism inherits only half of its genes from each parent, it can have fewer mutations than either parent.[11] This explanation was well supported by circumstantial and experimental evidence. Bell (1988a), Chao (1992) and Chao *et al.* (1992) have provided examples of populations of protozoa and viruses where Müller's ratchet is at work. In the first organisms, well supplied with food but deprived of sex in the laboratory, their populations showed a fast decline in fitness and a rapid accumulation of genetic defects that could be halted by sex. But these experiments also showed that even occasional sex would be enough to stop the ratchet. It is not necessary to completely give asexual reproduction up, yet most organisms are obligate sexuals. Kondrashov (1982), the other big exponent and leader of genetic theories, suggested an ex-

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[11] *E.g.* one of the expected genotypes from the cross $A_mB_w \times A_wB_m$ is A_wB_w, where the subscript m denotes a mutation and the subscript w denotes a non-mutant 'wild-type' gene. This example is provided by Mogie.

planation for this: asexual organisms have few mutations each, while sexual ones may have a few or many or anything in between. Thus, for example, when an asexual dies without reproducing, it only removes a few deleterious mutations from the gene pool. Those sexuals that carry many deleterious mutations are more likely to die without reproducing than those that carry fewer and take these mutations with them. Sex purges deleterious mutations out of the gene pool more efficiently than asexual reproduction.

The major criticism of both lines of genetic explanations is that even if they were true, which is not clear in all instances of sex, they would take too long to show the benefits of sex. Any asexual competitor would outnumber its sexual counterparts long before sex could accomplish its purging duty. Moreover, some organisms where asexual reproduction is common, *e.g.* bacteria, have low mutation rates. Neither does Müller's ratchet appear to work among them, nor do they seem to require Kondrashov's purge. One of Kondrashov's critics, W.D. Hamilton (1990), wrote of this purging role that sex was:

> "...a cumbersome strange tool to have evolved for a housekeeping role."[12]

The mention of W.D. Hamilton takes this work into the ecological theories of sex. However, his were not the first explanations of this type and thus a brief historical survey will be given. It is fair to say that the ecological debate about sex arose from the group *vs.* individual selection arguments. Although Williams had managed to prove beyond any reasonable doubt that collective benefits may be the result of selfish actions purely promoted by individual interests, and thus proved that group selection was just a mirage, he could not explain sex in the light of individual-based selection. Sexual reproduction seemed to be the only exception to this rule. This prompted him to look for a suitable explanation. His argument, now surpassed, came to be known as the lottery models for sex. Before explaining these models in more detail, it should be mentioned that Maynard Smith (1978) kept a pluralist approach, as he also saw in sex benefits for the species rather than the individual. Williams established a link between sexual reproduction and uncertain environmental conditions. In his Aphid-Rotifer model he looks at organisms that reproduce asexually throughout several generations but resort to sexual reproduction when the environment of their populations change. For aphids, the winter comes. For rotifers it is drought. At that point females mix their genes with those of males and resistant structures

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[12] Hamilton, W.D. (1990) Memes of Haldane and Jayakar in a theory of sex, p.30.

are produced that will survive until favourable conditions are back. Another instance of environmental uncertainty was provided by dispersal of propagules. Williams observed, in his Strawberry-Coral model, that certain organisms usually 'reproduce'[13] by extending asexually produced runners or branches that invade their immediate surroundings. When they are to invade new territory, then sexually produced seed and planulae, respectively, are sent away from the parent. These long-dispersing propagules would, according to Williams, most certainly face different conditions to those of the parental neighbourhood where they were produced. Yet another of his models, the Elm-Oyster model, compared environmental uncertainty to a saturated environment that is full of fiercely competing siblings, as it is experienced by the progeny of elms and oysters. Thousands of tiny young will have to fight, and most probably die, before the survivors find space where they can develop into fully grown adults. All these models are in his book *Sex and Evolution* (1975). So, for Williams, sex overcame its costs by ensuring diverse offspring, some of which would be able to adapt to whatever environment was found. The more uniform progeny of asexuals would be at a disadvantage with such environmental heterogeneity. The analogy to a lottery or raffle is that sex is more likely to have the winning ticket among many different ones than asexuals are with many copies of the same ticket (Greenwood and Adams, 1987).

Nonetheless, biologists did not completely accept the lottery explanation for sex. They counter argued that not all organisms produce offspring that will necessarily face uncertain environmental conditions. But the ultimate test, and demise, of this theory came in 1982, when G. Bell decided to confront the lottery models with the facts. According to Williams' conclusions, sexual reproduction should be favoured in harsh, unstable or unpredictable environments and among short-lived and small organisms which produce lots of offspring. Bell found the opposite phenomenon: asexual species tend to live at higher latitudes and altitudes, which are harsher environments than the central, towards-the-tropics areas where sexual species are so common. This pattern of geographic distribution of sexual and asexual forms is well documented in populations of flowering plants such as those of *Taraxacum* (Stebbins, 1950; Richards, 1973; Mogie, 1992; van Baarlen *et al.*, 2000)) or *Towsendia* (Bierzychudek, 1985, 1987b), and also in populations of animals (Glesner and Tilman, 1978; Daly and Wilson, 1983). From his comparative analysis, Bell concluded that sexual organisms, which live

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[13] According to the definitions in the previous section of this chapter, this would be considered growth rather than reproduction, but that was not Williams' point of view.

in stable environments, have the advantage of producing diversified offspring that may adapt to different niches so as to avoid competition in a saturated habitat, or 'tangled bank', as he called his theory.

The tangled bank theory was in turn put to the test by Austin Burt. A student of Bell's, he noticed that the tangled bank implied that sexual reproduction should be common among organisms that produce many small offspring that will fiercely compete with their siblings to get hold of a niche. The theory does not fit the facts either. Burt did his comparative study among mammals, looking at how much recombination takes place at reproduction in different species. He concluded that sex has little to do with the number of offspring or their size. However, Burt noticed that there was a relation between the generation length and the amount of recombination. More complex and longer-lived organisms, those that reach maturity later in their life cycle, tend to do more genetic mixing than others (Burt and Bell, 1987). Burt's study differs from previous works in that it takes an approach that is close to what is now perhaps the most accepted of the ecological theories of sex. His predecessors had in some way or another implied that it pays to diversify and sex is the vehicle for that. But in all their theories, the rewards of having the right lottery number, or adapting to the niche that nobody else could take, had to be large to overcome the costs of sex.

As it begins to be customary in this historical overview, it is necessary to look back in time, at a different idea in evolutionary biology. This time it is the Red Queen, first discussed in 1973. The author of this 'new evolutionary law'[14] is Leigh van Valen. While studying marine fossils, he discovered that species go extinct randomly. How old their lineages are has little influence on their probabilities of extinction or survival. This was in contradiction with how the interpretation of Darwin's ideas had itself evolved. There was always the belief that species adapt to their environment as they are gradually selected by it, so van Valen's idea that they never get any better, or worse, at surviving, was rejected. Thirty years later, however, the Red Queen is widely accepted and has found her niche in the explanations for sex. In brief, according to the Red Queen hypothesis, it does pay to diversify, but the main cause selecting for diversification is not the abiotic environment. Rather, it is necessary to keep up with competitors, predators, and pathogens, the environment that is subject to the same selective pressures and is thus constantly changing. Burt's observation fits particularly well into the host-parasite relationship. Parasites need to adapt to their hosts. They normally have short life cycles and go through many generations in just one generation of the

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[14] His manuscript actually bears this title: van Valen, L. (1973) A new evolutionary law.

host. So, the latter is under enormous pressure to have the right defences. The longer an organism lives, the more chances its parasites have to break through its defences. Apparently, sex provides the amount of variation that host-parasite interactions seem to demand.

Evidence for the connection between disease and sex that strongly supports the case of the Red Queen has arisen from a wide variety of sources: from experiments with mice to experiments with computers, from J.B.S. Haldane back in 1949 to W.D. Hamilton since the 1980s. Haldane was the first to hint at this connection when he suggested that:

> "... [heterogeneity] may play a part in disease resistance, a particular race of bacteria or virus being adapted to individuals of a certain range of biochemical constitutions, while other constitutions are relatively resistant."[15]

This idea was later developed by Jaenike (1978), Hamilton (1980, 1993), Bremermann (1980), Bell (1982), Tooby (1982) and Seger and Hamilton (1988). They all noticed that ***heterozygosity*** and ***polymorphism*** are closely associated with sex. These mechanisms make sure that many versions of the same gene are present, both at the individual and the population level. They also noticed that genes involved in disease resistance are among the most diverse in a species, the more so the more recombination is present (humans have more than mice, for example). According to Hamilton *et al.* (1990), the need to resist diseases could also answer for the fact that some polymorphisms are very ancient, as if genes to invent defences were never made completely obsolete. In computer simulations of their theory, these authors have shown that parasites adapt to the defences of the host and that old defence mechanisms can be brought back into play several generations later, when the parasites are busy breaking through a more common and recent defence mechanism. Also in these computer experiments, before the introduction of parasites, with all other factors being equal, the asexual component of a mixed population would always predominate. Experimental evidence supporting the sex-disease connection has come from the work of Bell and Burt (1990), where they showed that the presence of parasite-like entities such as a B-chromosome induces more recombination. Potts *et al.*'s (1991) experiments with mice showed that these animals, guided by their olfactory sense, mate with individuals that carry disease-resistance genes (genes coding for ***histocompatibility*** factors) which they do not possess, thus ensuring the production of offspring with different defence mechanisms.

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[15] Haldane, J.B.S. (1949) Disease and Evolution, p. 71.

In a sense, all three types of ecological theory seem to be able to explain sex to a certain extent. A thorough comparison of all three kinds of ecological theories of sex, —the lottery models, the tangled bank and the Red Queen,— was made in the 1990s, in experiments with populations of snails in New Zealand and with fish in Mexico by C.M. Lively, R.C. Vrijenhoek and their colleagues.

In the 1980s, both Lively and Vrijenhoek started their research on populations of snails (*Potamopyrgus antipodarum*) and fish (*Poeciliopsis occidentalis*), respectively, where sexual and asexual conspecifics coexist. Lively wanted to investigate the host-parasite relationship between *Potamopyrgus antipodarum* and its castrating parasite, a trematode called *Microphallus.* In New Zealand, some populations of this fresh water snail live in streams and others in lakes; in some there are only parthenogenetic females while in others there are males and females that have sex. Lively's hypothesis was that if environmental uncertainty (lottery models) was the predominant factor in the evolution of sex, this reproductive mode would be favoured in unstable environments such as streams. If competition was the driving force behind sex (tangled bank), then stable and saturated environments such as lakes would have more sexual varieties in them. Sex and parasites were to be found in lakes, so it was easy to discard the lottery explanations. But it was still necessary to compare the tangled bank against the Red Queen. If the latter was to be favoured, he hoped to find more sex where there were more *Microphallus* (Lively, 1987). Transplant experiments showed that *Microphallus* is indeed adapted to its host, being easier for the parasite to attack hosts in its lake of origin. Snails in different lakes have different defence mechanisms, so the transplanted parasite is initially at a disadvantage (Lively and Dybdahl 2000; Krist *et al.*, 2000; Lively, 2001; Lively and Jokela, 2002). Vrijenhoek, on his part, was interested in inheritance and variation mechanisms, as well as evidence for Müller's ratchet in asexually reproducing fish (*Poeciliopsis*) (Leslie and Vrijenhoek, 1980; Spinella and Vrijenhoek, 1982). He later got interested in the ecology and genetics of populations of *Poeciliopsis occidentalis* exhibiting both sexual and asexual breeding systems (Vrijenhoek and Lerman, 1982; Vrijenhoek, 1984; Schenk and Vrijenhoek, 1986). The experiments of Lively and Vrijenhoek with populations of *Poeciliopsis occidentalis* (or topminnows) in Mexico provided astonishing evidence favouring the Red Queen. The asexual varieties are triploid hybrids whose females reproduce asexually, although they require a sperm donor (a form of asexual reproduction known as ***pseudogamy***). Different clonal lineages may coexist, as do sexual and asexual forms. These fish are parasitised by a worm (*Uvulifer sp.*), which transmits black-spot disease.

Sexual forms (*P. monacha*) are less infected than their asexual counterparts (*P. 2monacha-lucida*). In those pools where different types of clones are present, the most common is the most infested. But the crucial evidence came from a pool that had been recolonised after a severe drought. Its population was highly inbred and sexual individuals were more affected than those of the clonal lines. However, after the introduction of sexual individuals from another pool, sexuals rapidly recovered and black-spot disease became more common among the clones (Lively *et al.*, 1990; Craddock *et al.*, 1993).

Despite all the favourable evidence, the Red Queen theory of sex has not remained unquestioned either. The main criticism to the parasite theories of sex is that they seem to require cycling behaviour with the right timing between the host and its parasites (Bell and Maynard Smith, 1987), or that the parasites have severe effects on their hosts' fitness (May and Anderson, 1990; Howard and Lively, 1994), or that they imply rank order truncation selection — only the healthiest hosts can reproduce (Hamilton *et al.*, 1990). Bierzychudek (1987a) noticed that if a theory to explain sex is consistent with the facts, it cannot be concluded that it was the ultimate cause. Similar to what happened with the ecological theories, for Bierzychudek it was impossible to discern which among the molecular, mutational or ecological approaches was the right one. By the late 1990s the mood had changed. Researchers did not seem to be looking for the 'rightful' approach, but calling for a pluralist one, a view that, as was noted before, Maynard Smith had more or less kept since his first involvement in the problem back in the 1970s. When Maynard Smith published his book *The Evolution of Sex*, in 1978, he kept an open mind to different points of view. For instance, he made clear that although he did not believe that traits evolved for the benefit of the species, the importance of group or individual selection for sex was difficult to assess. In his later works he looked both at the influence of a changing environment and mutations as the causes for the maintenance of sex (Bell and Maynard Smith, 1987; Maynard Smith, 1988). One of the strongest enthusiasts of the Red Queen theory, C.M. Lively, was among the first to notice that other mechanisms may also play a role (Lively and Howard, 1994; Howard and Lively, 1998). Studies like his on fresh water snails had the drawback that they were intent on providing evidence for or against a certain approach. Those were inference studies and could be missing the crucial observation that sex may be favoured by the interaction of several mechanisms, such as the presence of parasites and the accumulation of mutations. The simulation models he developed with Howard showed that it was indeed so. A few years later, his name was to appear in a review advocating for a pluralist approach to explaining sex and the associated process of genetic recombination (West *et al.*, 1999). The authors of this article consider that a pluralist approach is advantageous because it is possible that multiple mechanisms may be providing an advantage to sex and that more than one mechanism may be required to balance the two-fold cost of sex. Moreover, if such mechanisms were not only acting simultaneously, but also synergistically, any other approach would fail to capture this effect. A pluralist approach could also encourage experimental work to estimate parameters rather than to discard or support a given approach. The authors explain how the Red Queen and the mutational hypotheses, Müller's ratchet and Kondrashov's, complement rather than contradict each other. They also give evidence for their arguments from studies in plants (Kelley *et al.*, 1988; Kelley, 1994), apart from the results obtained in the simulation models by Howard and Lively. This article was included in the November issue of volume 12 (1999) of the *Journal of Evolutionary Biology.* The entire issue was dedicated to the evolution of sex. And so the discussion moved into the 21st century. Within the pluralist frame of mind, a PhD summer school and symposium were organised in Groningen in 2000 by Franz Weissing. All currents of thought and topics related to the evolution of sex were represented in the talks and posters participating in those meetings. Although they were classified into works related to evolution of sex (EOS), sex allocation and sex determination (SAD), sexual selection and conflicts between the sexes (SSC) and other 'sexy' topics (OST), it was the emphasis of the meetings to spark a discussion where people put forward controversial theses (*e.g.* Weissing's: "The evolution and stability of sexual reproduction is still a mystery; no real progress has been made in the last 30 years") and the other participants, from their diverse areas of expertise, may express their point of view. In this way people would spare a thought, and perhaps contribute, to a question that had never occupied them before.

As recently as April 2002, *Nature*, one of the most influential scientific journals, dedicated one of its special issues to the genetic research on the evolution of sex. Nature Reviews Genetics contains five articles on different aspects of this vast field of enquiry, three of which are centred on explaining the advantages of sexual recombination. For geneticists as well, the ubiquity of sexual reproduction is "one of the most enduring puzzles in evolutionary biology" (Otto and Lenormand, 2002). Their curiosity is fueled by recent technological advances, such as the use of better genetic markers, that allow for more accuracy in calculations of ***mutational load***, amount of ***crossing over*** between chromosomes and insertion of neutral mutations. They can now understand better the role played by genetic recombination in reducing accumulation of deleterious mutations and put the mutation-based explanations of sex to the test. They are also intrigued by the maintenance of ancient asexual lineages, such as the order Bdelloidea of rotifers, which seem to show evolution despite having been asexual for some 80 million years. Maynard Smith called these organisms "an evolutionary scandal"[16] This has been followed by the discovery that there is genetic variation among many other asexual organisms. April 2002 also saw the meeting of these scientists in London. *Intraclonal Genetic Variation: Ecological and Evolutionary Aspects* was the title of a two-day series of talks at the Linnean Society.

A quick search in the Web of Science, or any other database of scientific publications, will make clear that most of the names hitherto mentioned are still actively pursuing an explanation for sex, that elusive queen of evolutionary questions. The few years not covered in detail here have seen yet another wealth of articles on the topic, and the trend shows no signs of slowing down (see, for example, the works of J. Peck, D. Waxman and L. Hurst). Perhaps it is adventurous to say that Lewis Carroll was not thinking of the costs of sex when he wrote *Through The Looking Glass and What Alice Found There*, but the following quote from his book beautifully summarises what has been presented so far:

> "Well, in *our* country, said Alice, still panting a little, "you'd generally get to somewhere else — if you ran very fast for a long time as we've been doing."
>
> "A slow sort of country!" said the [Red] Queen. "Now, *here*, you see, it takes all the running *you* can do, to keep in the same place. If you want to get somewhere else, you must run at least **twice**[17] as fast as that!"[18]

1.3 What this work is about

The previous section may have given the reader an idea of how interesting and complex a problem the evolution and maintenance of sex are for evolutionary biologists, ecologists and geneticists alike. The "queen of evolutionary problems" has also aroused the curiosity of theoreticians and mathematicians, who, since

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[16] Maynard Smith, J. (1986) Contemplating life without sex, p. 301.

[17] Unlike Carroll's original italics, this bold emphasis is made by the author of this thesis.

[18] Gardner, M., ed. (1970) *The Annotated Alice.* London: Penguin. p.210. Carroll's original reference is given in the bibliography.

Crow and Kimura in 1965, have produced several models trying to explain the costs and advantages of sex. Less has been done to understand these two factors, costs and advantages, in the various forms of asexual reproduction (Mogie, 1992). Although most models have centred around finding conditions for the prevalence of either reproductive strategy, the coexistence of sexual and asexual relatives is common in natural populations (*e.g.* species within the genera *Taraxacum* and *Antennaria,* see Bierzychudek 1987b). Populations consisting of a mixture of sexually and asexually reproducing individuals offer a good opportunity to study the advantages and costs of both reproductive modes, yet only a few authors have considered the temporal dynamics of this kind of population (Charlesworth, 1980; Bell, 1982; Uyenoyama, 1984, 1985, 1986; Hamilton *et al.*, 1990; Roughgarden, 1991). Most of these models consider that sexually and asexually derived offspring are equally viable, or their fitness is assessed according to the reproductive mode they exhibit, not to their origin. That is to say, sexually derived but asexual offspring are as viable as their clonal siblings. Strange as this last sentence may sound, asexual individuals may sire offspring. This is particularly so in flowering plants. There, ample evidence suggests that all extant asexual taxa are descended from hermaphrodite sexual ancestors. In these species, asexual reproduction occurs via the female function, but male function, and thus the ability for sexual reproduction, is retained. In this way, pollen from asexuals may compete with that of sexuals for the fertilisation of eggs, making asexuals successful male parents (Mogie, 1992). Another feature of these models for mixed populations is that asexual individuals are considered to be either sterile in the male function, or as functional as their sexual counterparts. That is, they do not produce male gametes at all, or they produce as many as sexuals do. Finally, the fertility of these asexual male gametes, if they are produced, is considered to be equal to that of male gametes produced by sexuals. Working with these assumptions, these models have concluded that a stable polymorphism (the coexistence of sexual and asexual reproduction within a population) will not occur[19].

By way of an illustration, the now classic models by Maynard Smith and Charlesworth are briefly discussed here. Maynard Smith presented the cost of sex as the cost of producing males, and showed that it is two-fold, using the following reasoning: consider a population with equal numbers of females (N_f) and males (N_m.) Assume that after a dominant mutation, a small number of asexual females (n_a) is produced in the population. These females do not experience a reduction in fertility, producing the same k, $k > 0$, eggs as their sexual counterparts, or

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[19] This statement includes Hamilton *et al.*'s model before the introduction of parasites.

in reproductive success (a fraction S, $0 \leq S \leq 1$ of the progeny is successful for both sexual and asexual females), as a result of their asexual reproductive mode. Their offspring are identical to the mother and develop by parthenogenesis from the eggs produced by the asexual mother. As a result of these assumptions, the progeny generation will include Skn_a asexual clones, all female, $0.5SkN_f$ sexually derived females and $0.5SkN_f$ sexually derived males. It is immediately seen that half of the reproductive resources of sexual females has been invested in the production of males. In one generation only, the proportion of asexual females in the population has increased from $\frac{n_a}{N_f+N_m+n_a}$ to $\frac{Skn_a}{0.5SkN_f+0.5SkN_m+Skn_a}$. Since n_a was small compared to the total of sexuals in the population, this increase approximates a doubling in the presence of asexuals. Hence Maynard Smith's two-fold cost of sex due to the production of males. In his model, asexual females will replace sexual females and males.

For a population of hermaphrodites, Charlesworth (1980) proposed a modified version of Maynard Smith's model which included a variable sex ratio r, for the frequency of males ($1 - r$ for the frequency of females; as opposed to Maynard Smith's $r = 0.5$) and differentiated fitnesses for outbred and inbred individuals. In Charlesworth's model, a fraction i of the matings in the population results in inbred progeny, and thus a fraction $1 - i$ of the matings produces outcrossed progeny. A measure d, $0 \leq d \leq 1$, of inbreeding depression is introduced. Hence, inbred progeny have a fitness of $1 - d$, compared to the value 1 for outcrossed progeny. In Charlesworth's model, asexuality arises from a dominant mutation in a diallelic system (ss) codifying reproductive mode. Therefore, individuals which acquire one copy of the mutant gene (sa) are asexual. It suffices to follow the evolution in time of the proportion of asexual females in the population. Let p_a be such proportion in a given generation; and let p'_a denote this quantity in the next generation. Then,

$$p'_a = \frac{p_a f}{p_a f + (1 - p_a)(1 - r)(1 - i(1 - f))},$$

where f corresponds to the fitness of the female in which the mutation first arose; that is, $f = 1 - d$ for an inbred female and $f = 1$ for an outbred female. Divide then by p_a. The ratio $\frac{p'_a}{p_a}$, when p_a is close to 0 (as it is when asexual mutants first appear), can be approximated by

$$\frac{1 - d}{(1 - r)(1 - id)}, \tag{1.1}$$

for an inbred female, and by

$$\frac{1}{1-r}, \tag{1.2}$$

for an outbred female, who inherits her fitness, equal to 1, to her asexual daughters. In both cases, the conditions for the fixation of the asexual type are obtained when $\frac{p'_a}{p_a} > 1$. The weighed mean of the values in (1.1)–(1.2) gives a measure of the net intensity of selection on asexual mutants. This value is given by $(1-r)^{-1}$. Thus, the initial advantage of an asexual mutation depends only on the sex ratio r. Notice that when $r = 0.5$, Maynard Smith's model is recovered. In both models the final outcome is the same: if asexuality arises, it displaces sexuality.

A more realistic variation of mathematical models for the temporal dynamics of populations mixed for reproductive mode was attempted by Joshi and Moody (1995, 1998). The novelty of their models is that they include these very important omissions of the past: 'Most asexual plants retain male function albeit at levels much lower than their sexual counterparts'[20]. In order to accomplish their task, they introduce a parameter n, $0 \leq n \leq 1$, that compares the male gamete output of asexuals to that of sexuals. The comparison allows for equality in the number of male gametes produced or for a reduced male function in asexuals, whose extreme case is the production of no male gametes at all. With the introduction of this parameter, the models of Joshi and Moody comprise previous models, but also a wide range of biological situations in between. There is also a parameter c, $0 \leq c \leq 1$, that compares the fertilisation success of an asexual male gamete to that of a sexual one. In their population, asexuality arises as a result of a mutation. They offer a complete analysis for the case when this mutation is dominant or recessive. The polymorphic steady state they find turns out to be unstable and, as in previous models, only one reproductive mode can prevail.

Britton and Mogie (1998) produced a model for the temporal dynamics of a mixed population of flowering plants where the parameter n disappears. The reason for this is that there is no evidence to support the statement that a shift to asexuality will affect the number of male gametes produced by an individual. Populations described in several articles, (*e.g.* Weinzierl *et al.*, 1998), where asexual individuals do produce a reduced number of male gametes compared to that produced by their sexual conspecifics, are populations upon which natural selection will have had time to act since the appearance of asexuals. It is possible that natural selection will favour a reduced male function in asexuals, but this by no means implies that reduced male function is an intrinsic feature of asexual

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[20] Joshi, A. and Moody, M. (1995) Male gamete output of asexuals and the dynamics of populations polymorphic for reproductive mode.

reproduction when it first arises in a population as a result of a mutation. Thus, they decide to make the allocation of resources to male and female function and the male gamete output of sexuals and asexuals equal. However, Britton and Mogie acknowledge that the quality of the pollen produced by an asexual plant may not be the same as that produced by a sexual plant. They classify asexually produced pollen into: a) inviable pollen that cannot fertilise an egg, even when it actually encounters it; b) pollen of low quality that will sire zygotes that will be aborted; and c) fully viable pollen, as viable as sexual pollen, that may carry a gene for sexuality or asexuality. As in all the previous models, Britton and Mogie assume the simplest of genetic mechanisms to determine reproductive mode: one locus and two alleles, s for sexual reproduction, a for asexual reproduction. The equations of their model reflect the different possible origins for sexual and asexual zygotes. Like those of their predecessors, their model cannot exhibit a stable polymorphic steady state that explains the coexistence of sexuality and asexuality in mixed populations. From Mogie's work (1992), they put forward the hypothesis that such an explanation must rest upon spatial considerations hitherto rarely considered in mathematical models of this phenomenon (for an exception, see Keeling and Rand, 1995). They produce a model that considers the spread of an asexual mutant in an originally all-sexual population. This is described by a diffusive process with a normal distribution of the new reproductive mode around a source (Britton and Mogie, 2001). As they point out, such an approach is not realistic due to the dispersal patterns exhibited by pollen and seeds, which in many species may be leptokurtic (Crawford, 1984). Their model cannot explain coexistence either, but they lead the way to new and more realistic approaches to the spatial dynamics of populations mixed for reproductive mode. Another important aspect of the Britton-and-Mogie spatial model is that they consider the role of male function in asexuals. It is shown that the effect of male function in asexuals is frequency-dependent and that it favours a resident against an invader, be it sexual or asexual. They also discuss the role the male function in asexuals may have in the geographic distribution of related sexual and asexual forms.

The reader may now appreciate that the coexistence of sexual and asexual forms has eluded all previous modelling efforts that rely solely on the interactions between sexual and asexual conspecifics[21]. Of course, getting coexistence of populations, or reproductive modes in this case, is not the goal *per se*. However, there is a problem when, given that the coexistence of sexual and asexual forms within the same species is a well documented fact, mathematical models produced

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[21] Hamilton *et al.*'s and Keeling and Rand's models involve the presence of parasites.

so far overwhelmingly predict that only one mode can prevail. This leads to the following considerations: Are sexual and asexual relatives really coexisting, in the sense that they exhibit a stable polymorphism? Is it the case that the observed coexistence is just a step in a long evolutionary process that shall end as predicted in previous models: in the prevalence of either morph but not their coexistence? Or is it that mathematical models are failing to capture the coexistence of sexual and asexual relatives? If so, why? The work presented in the following chapters seeks answers to these questions. Therein lies the biological significance of this piece of research: it attempts to find a model, a spatial model, that describes or predicts the real world. Factors other than the interactions between the sexual and asexual components of a mixed population of angiosperms (flowering plants), and the spatial implications of the ecology of pollination and seed dispersal, will not be invoked. Despite the popular genetic trend, this work shall assume only the simplest of genetic mechanisms, thus inscribing itself in the framework of population ecology rather than genetics. The importance of and need for spatial models, by the way, has also been remarked by geneticists as a way of embracing more of the complexities of the real world (Otto and Lenormand, 2002).

1.4 Modelling assumptions

The purpose of this section is to outline and discuss the main biological aspects that will be taken into account, as well as their translation into modelling assumptions, in the models that comprise this thesis. After the historical and literary review made in the previous section, it will hopefully be clear why these, and only these, assumptions are made. This is important as it fully states the range of description and applicability of the models.

1.4.1 Simultaneous hermaphroditism

There is widespread evidence to suggest that extant asexual flowering plants have descended from sexual ancestors (Gustafsson, 1946-47). For example, they still exhibit traits associated with sexual reproduction, such as petals and nectar (Richards, 1973). It is widely accepted that most extant asexual taxa of flowering plants are descended from cosexual (*i.e.* hermaphrodite) ancestors and that most of them have retained male function (Mogie, 1992). Furthermore, it is believed that other sexual reproductive strategies in angiosperms, such as ***dioecy***, ***gynodioecy*** and ***androdioecy***, have evolved in hermaphroditic populations (Barrett, 2002). Keeping this fact in mind, it can simply and realistically be assumed that the individuals in the model population are ***simultaneous hermaphrodites***[22]. Their ability to function both as male and female at any given time will avoid consideration having to be given to the ratio of genders, more commonly referred to as sex ratio, in the model population. Moreover, an asexual can easily be identified with a cosexual whose female function has been modified to produce eggs that will develop into a new individual without fertilisation, but which has retained some level of male function. Therefore, the eggs produced by these individuals will not enter the contest for fertilisation, while the male gametes they produce will be able to fertilise eggs produced by the sexual component of the population. This assumption simplifies the modelling task ahead but is in no way a constraint: other ecological instances of sex can be easily represented by this population of simultaneous hermaphrodites. Dioecy, for example, can thus be regarded as a special case where the female and the male functions are packaged in separate individuals (Roughgarden, 1991).

1.4.2 Mating regime

When concerned only with the temporal dynamics of the population under study, random mating is the best assumption that can be made for it implies no spatial pattern. However, the mechanisms of pollen dispersal will make it necessary to introduce other kinds of mating regimes, or rather possibilities, with intrinsic spatial distributions. Populations of flowering plants are often insect-pollinated. Insects move from one flower to its near neighbours (Bertin, 1988), which in terms of paternity means that most flowering plants interact successfully with a small number of pollen donors. Meagher (1986) gives an estimate of less than six actual mates per individual in the willow herb *Chamaelirium luteum.*

Given that a population of simultaneous hermaphrodites will be considered, a few words about selfing as a mating regime are useful before going on. Although there are some examples in nature of simultaneous hermaphrodites which fertilise their own eggs, most populations have evolved mechanisms to avoid this possibility, and thus inbreeding. In those examples where selfing does occur, investment in male function is not high because the production of only a few male gametes is enough to guarantee reproductive success. This kind of auto-fertilising hermaphrodite needs only to produce one descendant to secure full representation of its genotype in the gene pool of the next generation. However, selfing is one of the two most important manifestations of sexual reproduction and, of the

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[22] As opposed to ***sequential.***

four forms of sexual reproduction identified by Mogie (1992), three are instances of selfing, these being ***autogamy*** and parthenogenetic and non-parthenogenetic ***automixis***. The importance of selfing as a possibility of mixis is made evident when considering the invasion of an asexual population by a sexual seed carried within its range by the wind. If not enough sexual seeds have been carried, the eggs of this sexual invader will most probably be fertilised by grains of pollen produced by its asexual neighbours, some of which carry a gene for asexuality that could turn its descendants into asexual individuals. Finally, selfing does occur and, when a shortage of neighbouring pollen takes place, selfed progeny are better than none at all. For completeness, the equations describing the model population will initially include selfing and will also allow for the inbreeding depression it may cause on zygotes so produced. However, given the rarity of this kind of fertilisation, and for the sake of mathematical simplicity, those terms will be removed from the equations before any analysis is performed.

1.4.3 Dispersal

In contrast to pollen dispersal by insects, a seed may be carried over long distances by the wind (*e.g.* the parachute-equipped seeds of *Asteraceae*) or by animals (Stiles, 1992), to places where it may have few neighbours sharing its reproductive mode, but also few potential competitors. Such a seed could give rise to a sexual individual that dies unfertilised, or could be the outpost of a successful invasion of new territory by its reproductive mode. It has been shown that the number of propagules experiencing long-distance dispersal is non-negligible and may play a very important role in the spread of a population. The statistical curves that best reflect the patterns of dispersal are those with less propagules around the centre of spread, and more in the tails of the distribution, as compared to traditionally assumed Gaussian patterns of dispersal. These more realistic patterns are called leptokurtic (see figure 1.1). Needless to say that the inclusion of long-range seed dispersal in a model will also imply spatial considerations, these being different to those that arise from short-range dispersal of pollen. The way in which these spatial factors are introduced is described in more detail in the relevant models.

1.4.4 Only one locus and two alleles

The genetic control, or determination, of asexuality is not a settled matter. However, many models assume a single locus and two alleles (e.g. Charlesworth, 1980; Joshi and Moody, 1995, 1998; Britton and Mogie, 1998, 2001). Thus, it

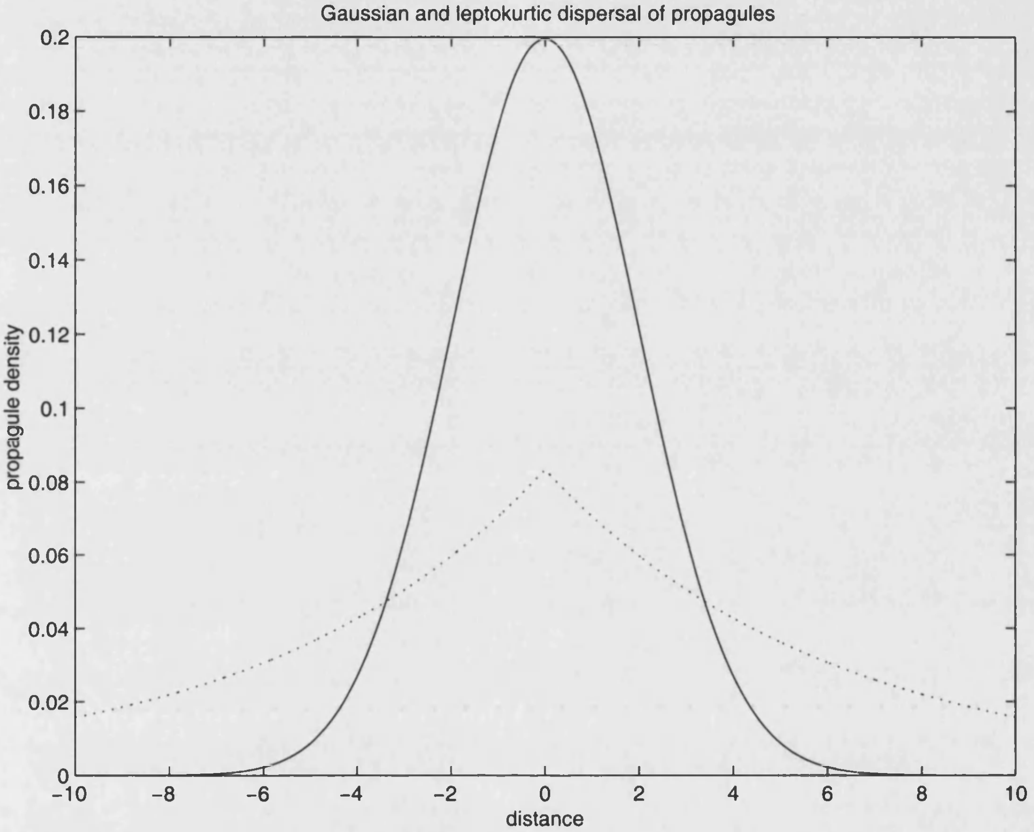

Figure 1.1: The figure shows a comparison of a Gaussian (solid line) *vs.* leptokurtic (dotted line) dispersal pattern. It can be seen how the number of propagules that experience long-range dispersal is greater for leptokurtic dispersal, which is why these patterns are also called ‘fat-tailed’.

will be assumed that in the mixed population under study, reproductive mode is determined by one diallelic locus, with allele s coding for sexuality and allele a for asexuality. This assumption simplifies the model while at the same time it enables track to be kept of a gene for sexuality or asexuality which arises via mutation in a population comprised of the other morph.

1.4.5 Population size

The model population is assumed to be large enough to enable random genetic drift to be ignored. To illustrate the effects of random genetic drift on the dynamics of the problem we are studying, we shall consider the following extract from *The Evolution of Asexual Reproduction in Plants*:

> The maintenance of asexuality in populations of cosexual heterospores (*e.g.* flowering plants) is not so problematic, as in this group there is a cost of sex which may be wholly attributable to the activity of male function of asexual forms. This will be the case whenever the transition from sexual reproduction to asexual reproduction does not result in asexual individuals achieving greater reproductive success than their sexual conspecifics via the female function. In this circumstance, if asexual individuals lack an effective male function, genes for sexual and for asexual reproduction may be selectively neutral with respect to each other. Consequently, an invading gene for asexual reproduction could achieve fixation through random genetic drift." [23]

1.4.6 Dealing with time

We assume that populations reproduce in discrete generations because the life histories of most of the taxa of mixed populations observed in nature allow us to do so (Mogie, 1992). It will be assumed that generations are non-overlapping, which would correspond with annual species. However, perennials that exhibit strong seasonality in flowering and dispersal of progeny are also well represented by this assumption. In other words, it is assumed that there is a discrete input to the population via reproductive/dispersal episodes. This assumption has traditionally been identified with models where time is discrete. The processes considered in this work develop through long periods of time, interglacial time scales, where annual changes may be barely perceptible. In particular, if weak

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[23] Mogie, M. *op. cit.*, p.123.

selection was assumed, it would be possible to study the system through continuous rather than discrete models, applying the corresponding mathematical techniques. The analyses in this work, however, remain restricted to discrete-time models, discussing continuous time where relevant. The conclusions that may be drawn from a discrete-time setting still show how changes taking place at a short time scale determine the long-term outcomes of the evolutionary processes of interest.

1.4.7 The viability of sexuals and asexuals

It has been widely argued that sexual individuals are better equipped than their asexual counterparts to track the environmental changes, challenges and threats the population faces because generation after generation they recombine their genomes and may thus record all these features of the environment around them. At least some members of the diverse progeny produced by sexuals could be strong enough to survive climatic changes or the attack of parasites that their parents or contemporaries could not (Crow, Bell, Maynard Smith and Seger and Hamilton in Michod and Levin, 1988). This advantage of sexuals may be regarded as a disadvantage for asexuals. In some instances of asexual reproduction, namely ***apomixis*** and ***adventitious embryony***, the female passes on her complete set of genes to her offspring, which enhances her fitness, but makes the asexual population more susceptible to parasites which have already managed to attack this particular genotype (Mogie, 1992). Nevertheless, asexuals can acquire mutations, or, if they have retained male function, incorporate new genetic information into their population through crosses with sexual individuals. In a mixed population where asexuals have retained male function, the progeny of sexuals may become asexual if the male gamete is provided by an asexual and carries a gene for asexuality. However some of the progeny sired by asexual individuals will be sexual if the male gamete does not carry the mutant gene (Mogie, 1992). Therefore, the progeny can be considered to be as viable as their reproductive mode dictates (Charlesworth, 1980), or as viable as their progenitors (Joshi and Moody, 1995). Each of these assumptions would give rise to different ecological scenarios. In these models, viabilities will be assigned to zygotes according to the way they were produced. Therefore, eggs that develop parthenogenetically will show the same probability of survival as their asexual mother. Sexual eggs fertilised by a male gamete, regardless of the origin of this gamete and the genetic information it carries, will be thought to have the viability of the sexual parent. In other words, zygotes having both a sexual mother and father will not have an advantage over those zygotes produced by a sexual mother and an asexual father.

1.4.8 Male function in asexuals

One aspect of the importance that male function has for asexuals is that they can incorporate new genes into their populations through crosses with sexual conspecifics. Thus, male gametes produced by asexuals may fertilise the eggs produced by sexual females and give rise to viable asexual progeny with a different genotype. This genotype will be added to the asexual component of the population and may make this component more resistant to environmental changes. Male gametes are also cheaper to produce, in energetic terms, and are therefore more numerous, than eggs. Male function allows an asexual genotype to 'conquer' new genetic territory as described above. That is, male function is determinant in the establishment of asexuality.

Additionally, male function may be determinant in the geographic distribution of related sexual and asexual forms. Although these forms may be ***sympatric***, they tend to occupy different ranges, with asexual forms extending over greater and often more rigorous landscapes. A first explanation for this pattern of distribution is that asexuals have been excluded from landscapes where sexual forms and their pathogens are well adapted. Another hypothesis finds that male function confers a superior colonising ability upon asexual individuals.

But male function is not always efficient in asexuals. It is often the case that in these individuals male meiosis is disturbed, resulting in reduced or partially reduced gametes which contribute to progeny which are inviable (Nogler, 1984; Asker and Jerling, 1992; Mogie, 1992). Also, some male gametes produced by asexuals are of such poor quality that, being sterile, they cannot outcompete male gametes produced by sexual individuals.

Mogie (1992) fully acknowledges the problems of asexually produced pollen regarding perturbed meiosis and poor quality. However, he gives no evidence to support the assumption that a shift to asexuality will reduce the male gamete output of a flowering plant. Furthermore, Mogie believes that populations found in nature where such reduced male gamete output is observed have this feature after natural selection has acted upon them and not as an immediate consequence of asexuality. Following these remarks, Britton and Mogie's (1998) approach will be used in this thesis. Thus, sexual and asexual forms will be considered to allocate the same amount of resources to male function. Pollen will not be a limiting resource as it will be assumed that enough male gametes are produced to fertilise all eggs produced by sexual females. Finally, although this is a paragraph about male function, let it be made clear that sexual and asexual females also allocate the same amount of resources to female function, that is, both morphs produce the same amount of eggs. This being the final assumption to be made, it is now time to move to the models themselves.

Acknowledgements: Many references had to be revised to put this chapter together. To find order among so many papers, as many discussions with Dr. Mogie were of invaluable help. So were his lecture notes on asexual reproduction and the maintenance of sex and the PhD thesis by François Delmotte, Évolution des modes de reproduction chez le puceron *Rhopalosiphum padi* (L.): apports de la génétique des populations et de la phylogenie moléculaire (ENSAR, 2001).

Chapter 2

Temporal Dynamics of Populations Mixed for Reproductive Mode: Sexuality *vs.* Asexuality

The first chapter has set the context where the models within this thesis will be inscribed. There, a summary was made about previous attempts to explain the evolution and maintenance of sex. It was also explained how the coexistence of sexual and asexual forms poses another interesting question in evolutionary biology. This question has so far not been resolved unless external factors are invoked, *e.g.* interaction with parasites. More important perhaps, was the discussion about those biological aspects that cannot be overlooked in any modelling attempt to address this question. Hopefully, it was clearly established how these aspects are going to be treated in the models that follow. This second chapter comprises a model describing the temporal dynamics of a population of flowering plants where sexual and asexual conspecifics coexist. The common dandelion, *Taraxacum officinale*, offers a well-known example of this kind of population. The key assumption of this temporal-dynamics model is random mating. Having said that the consideration of spatial issues is vital to the study of populations mixed for reproductive mode, particularly when those populations consist of flowering plants, the development of a first model to describe the temporal dynamics of sexuality *vs.* asexuality may seem contradictory. This is not so. Although this first model is rather in itself a summary of previous models, it will be of much help in understanding how the issues discussed in the first chapter are translated into the mathematical language. It will be shown that this is a more general model that retrieves, under certain parameter restrictions, the results of previous, now classic models. Ultimately, this model will lay the foundations for the spatial models ahead.

2.1 Assumptions of the model and notation

Neglecting spatial effects, consider a ***panmictic*** population of simultaneous hermaphrodites originally sexual in their reproductive mode, where asexuality emerges as the result of a mutation. Moreover, assume that it emerges as a dominant trait. It suffices to consider this case as, according to Mogie (1992), there is evidence that although dominance is not absolute and is due to dosage effects, genes for asexuality are effectively dominant. Considering the case when this mutation is a recessive trait makes a model more complicated — two copies of the mutation would have to be acquired before asexuality is manifest — while results would not be qualitatively different. This is clear in the model by Joshi and Moody (1995), where the recessive case is considered. Therefore, in good accordance with the biology of asexuality and to keep the mathematical analysis simple, such case will not be considered. As said before, reproductive mode is considered to be determined by one locus and two alleles, s for sexuality and a for asexuality. Thus, individuals ss are the original sexual components of the population until a mutant sa, asexual, emerges. In this population there will be $N_s(t)$ sexual individuals and $N_a(t)$ asexual individuals present at a given time t (see ADULT PHASE in figure 2.1). In general, throughout this thesis the letters s and a will refer to sexuality and asexuality respectively. The gametes produced by sexual individuals carry only the s allele. Sexual eggs need to be fertilised by a male gamete in order to initiate a new individual. The siring male gamete may come from the same sexual individual that produced the egg (selfing), or from a sexual or asexual neighbour (outcrossing). Let i denote the fraction of sexual eggs that may be fertilised by male gametes from the same sexual individual. These eggs will not compete for male gametes from other individuals. But resulting zygotes may then suffer from inbreeding depression, denoted by d, $0 \leq d \leq 1$. Asexual individuals produce eggs that carry the same genetic information as the mother and that develop into new individuals without any need for fertilisation. They are also capable of producing male gametes that will compete with sexually produced male gametes for the fertilisation of sexual eggs. However, the male gametes produced by asexuals may not be as effective as those produced by sexuals. A fraction u of these male gametes will be considered inviable, that is, they may not fertilise eggs even when they come into contact with them. Thus, inviable male gametes do not exclude other male gametes from fertilising, but consume reproductive resources of the individual that produces this kind of male gametes and should therefore play a part in this model. Another fraction b of male gametes produced by sexuals is of poor quality. They may fertilise sexual eggs but the zygotes sired by them will most likely result in post-zygotic seed abortion (the loss of this fraction b is shown in GAMETIC PHASE and TO MATURITY NEXT ADULT PHASE in figure 2.1). Yet another fraction g_s is good quality male gametes that carry the s gene for sexuality and, finally, g_a is the fraction of good quality male gametes that carry a gene a for asexuality. The whole of the male gametes produced by asexual individuals are comprised within these four categories. k_m will denote the amount of resources that an individual allocates to male function, $0 \leq k_m$, while k_f, $0 \leq k_f$, will be the allocation of resources to female function — these resources are not necessarily measured in the same units. These numbers are assumed to be equal for both sexual and asexual individuals since there is no evidence to support the view that a shift to asexuality affects the potential gamete production of an individual (see GAMETIC PHASE in figure 2.1). However, sexually and asexually produced zygotes will not be considered equally viable. v_s will denote the probability of a sexually produced zygote reaching maturity, while v_a will denote the same for asexually produced offspring. Sexually produced zygotes certainly have genetic information different to that in the parental genotype, while asexual zygotes, sometimes referred to as ***clones***, may have their mother's genetic set-up. This differentiation renders the former more apt to resist environmental challenges, while the latter could, for instance, be attacked by a parasite or disease that has previously attacked the parental generation. Therefore, their viabilities are not necessarily the same (see TO MATURITY NEXT ADULT PHASE in figure 2.1). It will also be assumed that the population has a life history of discrete, non-overlapping generations. Finally, the population will be assumed to be large enough to enable the model to ignore the effects of random genetic drift.

2.2 Equations of the temporal dynamics model

With these assumptions and notation in hand, the equations for the number of sexual and asexual individuals in the next generation can be stated in the following way:

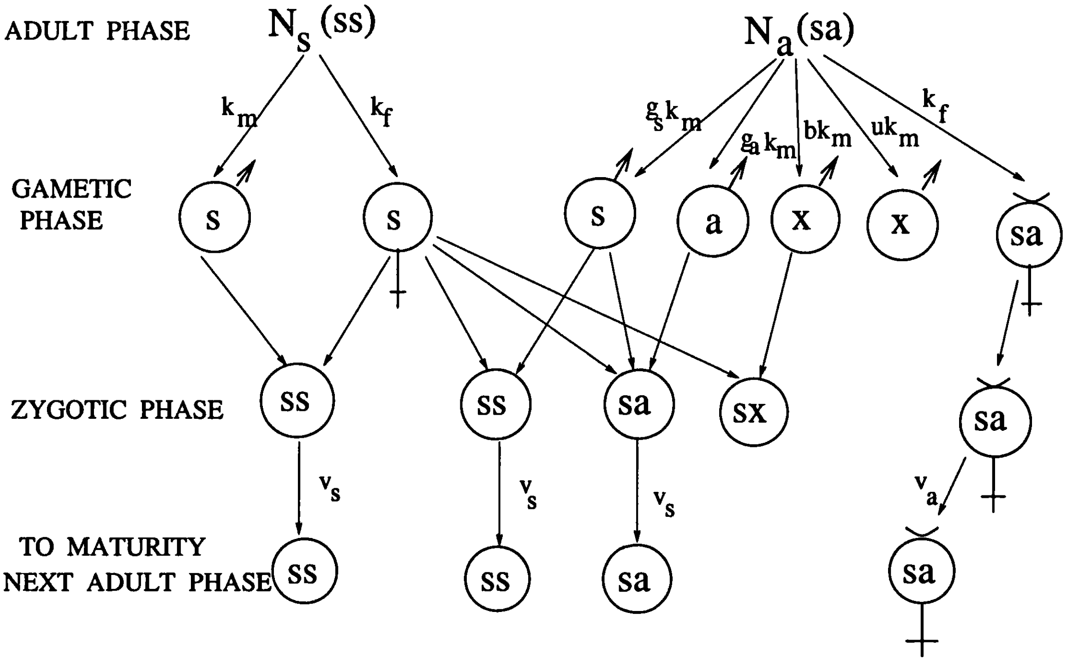

Figure 2.1: The figure shows a schematic description of the phases in the life history of the population of flowering plants in the model. It can be seen how the fraction u of inviable pollen produced by asexuals does not participate in the fertilisation of eggs, but does consume resources allocated to the male function. Also, it is possible to see how those zygotes sired by the fraction b of poor-quality pollen produced by asexuals are lost to post-zygotic seed abortion and do not reach the maturity phase. For simplicity, the figure does not show inbred progeny.

Adult Phase. At time t there are $N_s(t)$ sexual individuals and $N_a(t)$ asexual individuals.

Gametic Phase. Each sexual individual will produce k_f eggs and k_m male gametes. These gametes all carry an allele s that codes for sexuality. Asexual individuals also produce k_f eggs, which will be referred to as clones because they will develop into new individuals without fertilisation. These clones have genetic information sa. Asexuals produce as many male gametes as sexuals do, k_m per individual, but they are divided into four categories, u, b, g_s and g_a. Thus, uk_m are inviable male gametes, bk_m are male gametes of poor quality, g_sk_m are good quality male gametes that carry allele s for sexuality and g_ak_m are good quality male gametes that carry allele a for asexuality. In the end, there are $k_fN_s(t)$ eggs produced by sexuals requiring fertilisation to become progeny, $k_mN_s(t)$ male gametes produced by sexuals, $k_fN_a(t)$ asexually produced clones, and $(u+b+g_s+g_a)k_mN_a(t)$ male gametes of diverse qualities produced by asexuals. All these gametes will scramble to fuse and become zygotes, the initiating cells of the adults in the next generation.

Zygotic Phase. Eggs produced by sexuals need to be fertilised to initiate a new individual. It is assumed that enough male gametes are produced to fertilise all eggs. Some of these male gametes may have been produced by the same sexual individual providing the egg, in which case there is selfing. Let i be the proportion of zygotes which are the result of selfing. Alternatively, sexual eggs will also be fertilised by male gametes produced by other sexuals or by asexuals. Inviable male gametes in the u category do not fertilise eggs, even when they come into contact with them. Thus, only categories b, g_s and g_a are taken into account. $k_mN_s(t)+(1-u)k_mN_a(t)$ is the total number of male gametes that may fertilise eggs. Thus, there will be

$$(i)\ ik_fN_s(t)$$

sexual, ss, zygotes that are the product of selfing;

$$(ii)\ \frac{(1-i)k_fN_s(t)k_mN_s(t)}{k_mN_s(t)+(1-u)k_mN_a(t)}$$

sexual, ss, zygotes produced by the outcrossing of sexual individuals;

$$(iii)\ \frac{(1-i)k_fN_s(t)g_sk_mN_a(t)}{k_mN_s(t)+(1-u)k_mN_a(t)}$$

sexual *ss* zygotes produced by the outcrossing of a sexual egg and an asexual male gamete carrying allele s for sexuality;

$$(iv)\ \frac{(1-i)k_fN_s(t)g_ak_mN_a(t)}{k_mN_s(t)+(1-u)k_mN_a(t)}$$

asexual, *sa*, zygotes produced by the outcrossing of a sexual egg and an asexual male gamete carrying allele a for asexuality;

$$(v)\ \frac{(1-i)k_fN_s(t)bk_mN_a(t)}{k_mN_s(t)+(1-u)k_mN_a(t)}$$

zygotes which are the product of the outcrossing of sexual eggs with asexual male gametes of poor quality; and

$$(vi)\ k_fN_a(t)$$

asexual clones.

Maturity Phase. This phase is also the next adult generation. Those zygotes which mature become the individuals in the population at time $t+1$. It will be up to them to initiate a new reproductive episode. Of all the zygotes produced in the previous phase, those which were the product of selfing may suffer from inbreeding depression, d. In general, sexually produced zygotes have a viability v_s, while v_a is the viability of asexually produced progeny. Finally, eggs fertilised by male gametes of poor quality very often result in post-zygotic seed abortion. It will be assumed that those embryos do not make it to the maturity phase. That is why in v) above their genetic information could be ignored. The previous numbers are thus modified as follows:

$$(i)\ dv_sik_fN_s(t);$$

$$(ii)\ v_s\frac{(1-i)k_fN_s(t)k_mN_s(t)}{k_mN_s(t)+(1-u)k_mN_a(t)};$$

$$(iii)\ v_s\frac{(1-i)k_fN_s(t)g_sk_mN_a(t)}{k_mN_s(t)+(1-u)k_mN_a(t)};$$

$$(iv)\ v_s\frac{(1-i)k_fN_s(t)g_ak_mN_a(t)}{k_mN_s(t)+(1-u)k_mN_a(t)}$$

and

$$(v)\ v_ak_fN_a(t).$$

The previous description of the life history of the population allows the following equations to be derived:

$$N_s(t+1) = dv_s i k_f N_s(t) + v_s \frac{(1-i)k_f k_m N_s(t)^2}{k_m N_s(t) + (1-u)k_m N_a(t)}$$

$$+v_s \frac{(1-i)k_f k_m N_s(t) g_s N_a(t)}{k_m N_s(t) + (1-u)k_m N_a(t)} \tag{2.1}$$

$$N_a(t+1) = v_s \frac{(1-i)k_f N_s(t) g_a k_m N_a(t)}{k_m N_s(t) + (1-u)k_m N_a(t)} + v_a k_f N_a(t) \tag{2.2}$$

Notice that both equations clearly show how sexual and asexual individuals are sired. Sexuals have two possible origins: they are the result of a cross between a sexual egg and a sexual male gamete, which is written in the first two terms of (2.1). Within these terms, those sexuals who are the result of selfing can also be distinguished. The third addend of (2.1) counts those sexual individuals who result from a cross between a sexual egg and an asexual male gamete carrying the gene for sexuality. Similarly, asexuals can result from two processes: a cross between a sexual egg and an asexual male gamete carrying the gene for asexuality which is expressed by the first term in equation (2.2), or they are conceived as clones of the asexual mother and counted by the second term. It can be immediately noticed that for some values of k_f and k_m, the equations written above will eventually produce large numbers of each type. Populations do not increase their numbers indefinitely, on the other hand. It will be implicitly assumed that the sexual and asexual components of the populations are equally limited by environmental resources. Consequently, the mechanisms regulating the population do not appear in these or future equations. However, it is pertinent to discuss here how such regulation mechanism could be fitted into the model. Consider $\bar{N}$, an arbitrary carrying capacity for the environment where the species lives. When the total number of individuals, $N_s + N_a$, exceeds this quantity, then the variables $\bar{N}_s := N_s\bar{N}/(N_s + N_a)$ and $\bar{N}_a := N_a\bar{N}/(N_s + N_a)$ can be introduced. Notice, therefore, that the carrying capacity will not be exceeded in any generation. This could be interpreted as deaths of individuals due to overcrowding of the environment.

2.3 Intuitive approach to the analysis of the model

For the purposes of the mathematical analysis of the model, let $X(t)$ denote the quotient $\frac{N_s(t)}{N_a(t)}$, with $t \geq 0$. Then, due to (2.1) and (2.2), the following equality holds

$$\begin{aligned} X(t+1) &= \frac{dv_s iX(t)(X(t)+1-u)+v_s(1-i)X(t)(X(t)+g_s)}{v_s(1-i)g_aX(t)+v_a(X(t)+1-u)} \\ &= \frac{v_s(di+(1-i))X(t)^2+v_s((1-u)di+(1-i)g_s)X(t)}{(v_s(1-i)g_a+v_a)X(t)+v_a(1-u)} \end{aligned} \tag{2.3}$$

Notice that if the model with environmental restriction was to be considered, $\bar{X}(t) := \bar{N}_s(t)/\bar{N}_a(t)$ would be the variable under analysis and that $\bar{X}(t) = X(t)$. It is also straightforward to notice that the dynamic rule for $\bar{X}(t)$ would be the same as (2.3). Hence, no qualitative changes in the corresponding analysis are expected. Equation (2.3) can be thought of as the following recurrence relation

$$X_{t+1} = \frac{(\alpha X_t + \beta)X_t}{\gamma X_t + \delta}, \quad t \in \mathbb{N} \tag{2.4}$$

where $\alpha = v_s(di + (1-i))$; $\beta = v_s((1-u)di + (1-i)g_s)$; $\gamma = v_s(1-i)g_a + v_a$ and $\delta = v_a(1-u)$.

It is not always true that a discrete model can be embedded into its continuous-time formulation. Yet, as a way of gaining insight into the behaviour of the sequence X_t, a standard analysis of the continuously differentiable function $f(X)$, defined by the formula

$$f(X) = \frac{(\alpha X + \beta)X}{\gamma X + \delta},$$

will be used first; it will just be a geometric approach, to outline all different cases and results concerning the function $f(X)$ and, consequently, the behaviour of the sequence X_t. This is merely a heuristic argument. However, rigorous justification of such an intuitive approach will be given in the appendix, using well-known techniques for the analysis of real sequences.

To implement the programme described above, the function $f(X)$ will be represented as

$$f(X) = \frac{\alpha}{\gamma}X + \frac{1}{\gamma^2}(\beta\gamma - \alpha\delta) - \frac{\delta}{\gamma^3}(\beta\gamma - \alpha\delta)\left(X + \frac{\delta}{\gamma}\right)^{-1}. \tag{2.5}$$

Notice first that $f(0) = 0$. Secondly, the derivative of the function $f(X)$ is given by

$$f'(X) = \frac{\alpha}{\gamma} + \frac{\delta}{\gamma^3}(\beta\gamma - \alpha\delta)\left(X + \frac{\delta}{\gamma}\right)^{-2}. \tag{2.6}$$

Thus, notice that $f'(0) = \frac{\beta}{\delta}$. Furthermore,

$$f''(X) = -\frac{2\delta}{\gamma^3}(\beta\gamma - \alpha\delta)\left(X + \frac{\delta}{\gamma}\right)^{-3}. \tag{2.7}$$

In order to fully understand the dynamics of the relation (2.4) via the behaviour of the transformed function in (2.5), the following cases must be considered:

Case 1. $\beta\gamma - \alpha\delta < 0$, or, written in an alternative way, $\frac{\beta}{\delta} < \frac{\alpha}{\gamma}$. Then, the equality in (2.7) implies that $f''(X) > 0$ for all nonnegative values of X. It follows from here that the derivative $f'(X)$ is an increasing function. Since $f'(0) > 0$, one concludes that $f'(X)$ is positive for all X. Hence the function $f(X)$ is increasing.

It is now necessary to consider several cases within this first case:

Case 1a. $1 < \frac{\beta}{\delta} < \frac{\alpha}{\gamma}$. In this case, X_t tends to infinity as $t \to \infty$ and therefore $p_s(t) := \frac{N_s(t)}{N_s(t)+N_a(t)}$ tends to 1 with time. It is clear that $p_s(t)$ represents the fraction of sexual individuals in the population at time t. The fact that it tends to 1 means that the sexual component of the mixed population takes over its asexual counterpart. In other words, sexuality is fixed in a population showing this behaviour. An approximate graph of this sort of behaviour is given in figure 2.2.

Case 1b. $\frac{\beta}{\delta} < 1 < \frac{\alpha}{\gamma}$. In this case, an unstable steady state X^* can be found, given by the formula $X^* = \frac{\delta-\beta}{\alpha-\gamma}$. For any initial condition below the value X^*, the sequence X_t will decrease as $t \to \infty$ tending to 0 and asexuals will then be fixed. For an initial condition above the value X^*, the sequence X_t will increase as $t \to \infty$. Therefore, X_t will tend to infinity and sexuals will be fixed. Only if the initial condition happened to be exactly X^* would coexistence of both reproductive modes be observed, but having such a precise start is an event of probability zero. The behaviour of the sequence in this case is depicted in figure 2.3.

Case 1c. $\frac{\beta}{\delta} < \frac{\alpha}{\gamma} < 1$. Asexuals will take over the sexual component of the population as X_t tends to 0 when $n \to \infty$ and therefore $p_s(t)$ also tends to 0 with time. Asexuality prevails as the reproductive mode of a population showing this kind of behaviour. An approximate graph of f for this case looks as shown in figure 2.4.

As the reader can see, the strategy followed to study case 1 has been to investigate the behaviour of the system with respect to the relative positions of lines $Y = \frac{\alpha}{\gamma}X$, $Y = \frac{\beta}{\delta}X$ and $Y = X$ together with the corresponding cobweb diagram. This same strategy is used to study cases 2 and 3, where $\beta\gamma - \alpha\delta = 0$ and $\beta\gamma - \alpha\delta > 0$ respectively. The behaviour of the system is similar and results are obtained in a completely analogous manner which will not be repeated here.

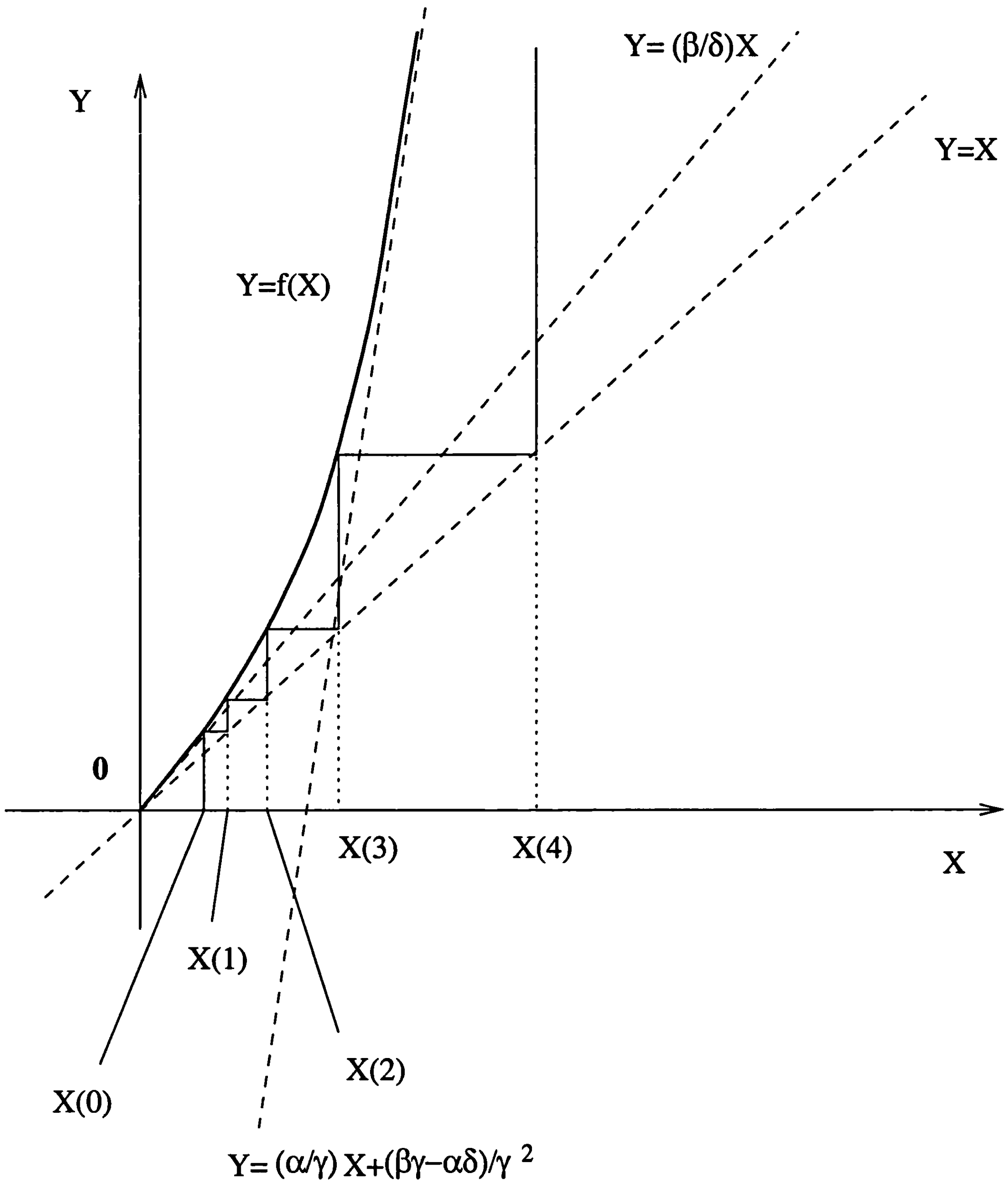

Figure 2.2: The graphic shows a cobweb diagram for the case when $1 < \frac{\beta}{\delta} < \frac{\alpha}{\gamma}$. The relations between the parameters are such that fixation of sexuality is observed.

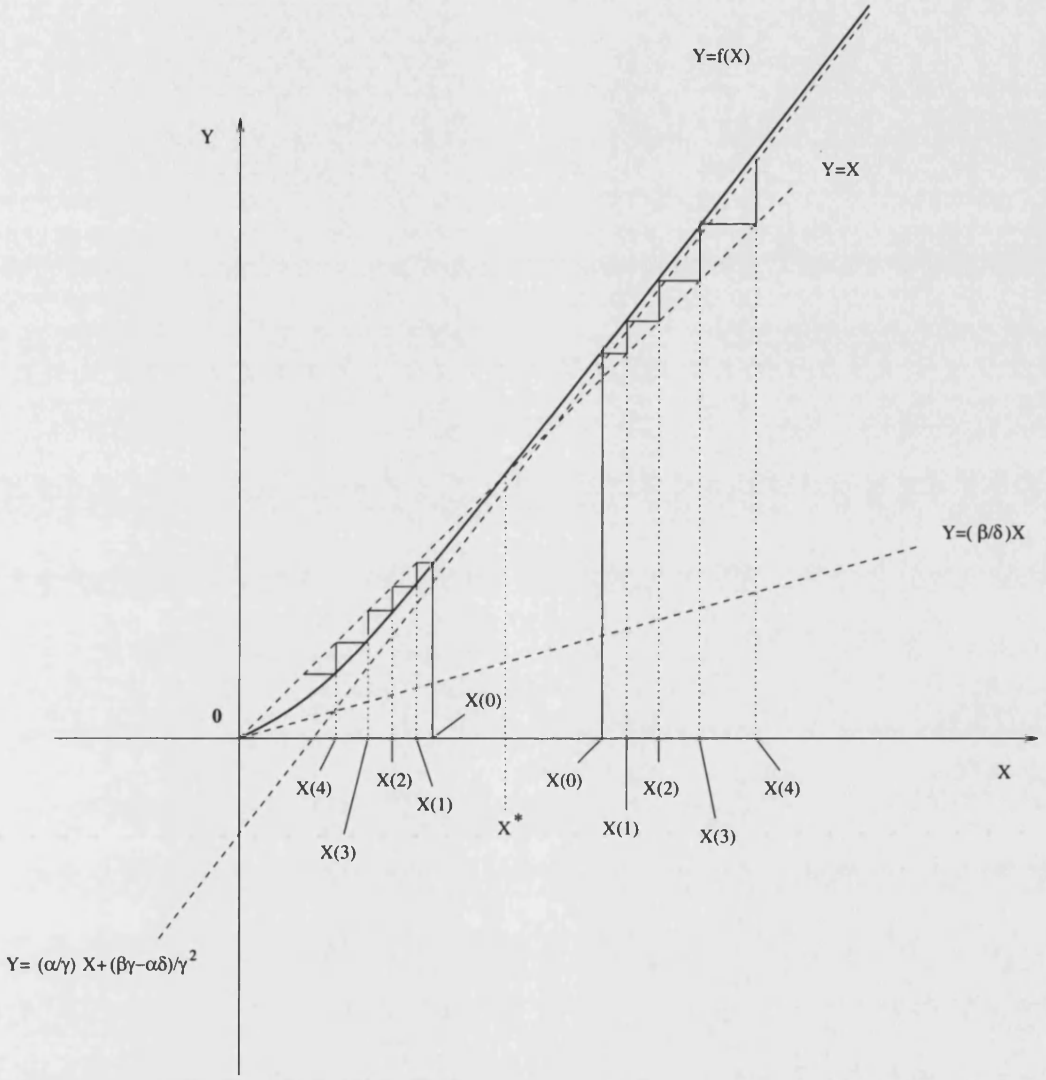

Figure 2.3: This figure corresponds to the case where $\frac{\beta}{\delta} < 1 < \frac{\alpha}{\gamma}$. It is possible to observe in this figure that any initial condition below X^* will tend to 0 under the behaviour of the dynamical system, while any initial condition above X^* will eventually tend to ∞.

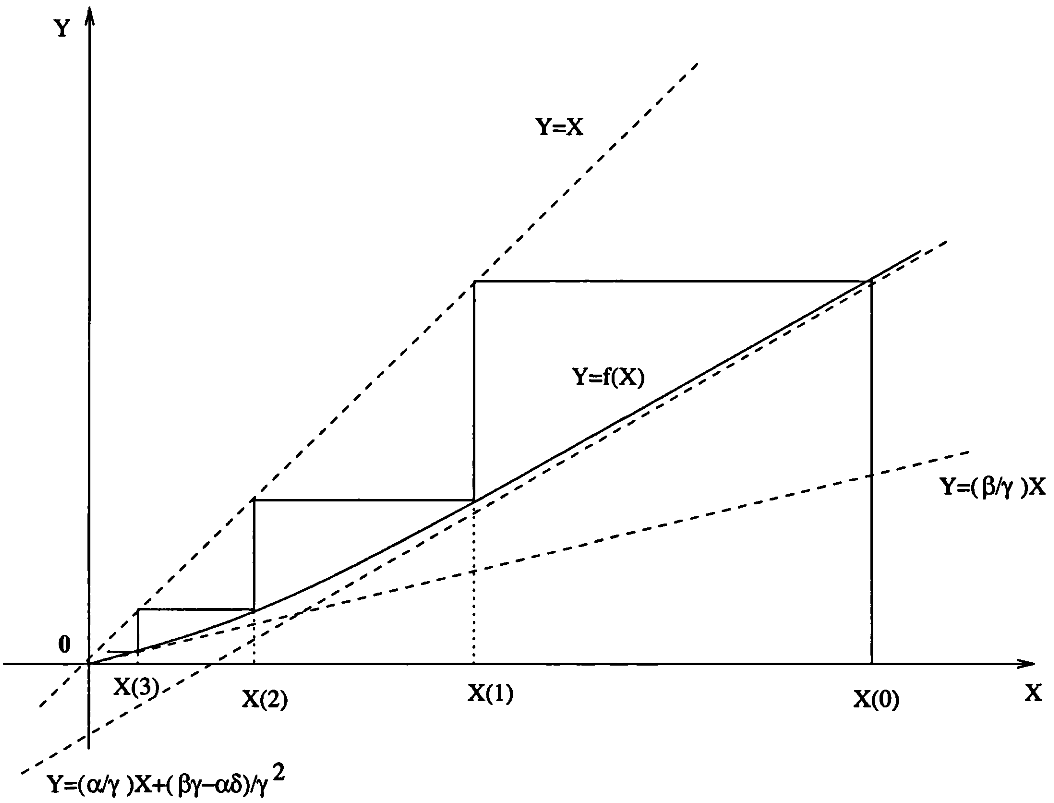

Figure 2.4: When $\frac{\beta}{\delta} < \frac{\alpha}{\gamma} < 1$, any initial condition will tend to 0 under the action of the dynamical system. In this parameter regime, asexuals are the dominant type in the population and eventually go to fixation.

There is, however, an interesting case:

$$\frac{\beta}{\delta} > 1 > \frac{\alpha}{\gamma}. \tag{2.8}$$

Notice that $X^* := \frac{\delta-\beta}{\alpha-\gamma}$ is now a stable steady state as shown in figure 2.5. This could imply the coexistence of sexual and asexual forms. A closer examination of the value X^* in terms of the biological parameters of the model leads to the following expression:

$$X^* = \frac{\delta - \beta}{\alpha - \gamma} = \frac{v_a(1-u) - v_s((1-u)di + (1-i)g_s)}{v_s(di + (1-i)) - v_s(1-i)g_a - v_a}.$$

Unfortunately, it is impossible to find values for parameters that satisfy the relations in (2.8). Recall that $\alpha < \gamma$ and $\delta < \beta$ in the case of where the stable steady state is found. These conditions mean that

$$v_s(di + (1-i) - (1-i)g_a) - v_a < 0 \tag{2.9}$$

and

$$v_a(1-u) - v_s((1-u)di + (1-i)g_s) < 0 \tag{2.10}$$

respectively. Let μ denote the quotient $\frac{v_s}{v_a}$. Then, from the inequalities (2.9) and (2.10), the value of μ must be such that

$$\mu < \frac{1}{di + (1-i)(1-g_a)} \tag{2.11}$$

and

$$\frac{1-u}{(1-u)di + (1-i)g_s} < \mu, \tag{2.12}$$

respectively. If a value μ satisfying the last two inequalities existed, then the inequality $\frac{1-u}{(1-u)di+(1-i)g_s} < \frac{1}{di+(1-i)(1-g_a)}$ would hold. This implies that $(1-u)(di+(1-i)(1-g_a)) < (1-u)di + (1-i)g_s$ and therefore $(1-g_a)(1-u) < g_s$. But, clearly, $(1-g_a)(1-u) > 1 - g_a - u > g_s$. Thus no value μ satisfying (2.11) and (2.12) at the same time can be found. Consequently, stable coexistence consistent with the parameters of the model does not occur. A formal discussion of this and all previous cases is offered in the appendix to this chapter.

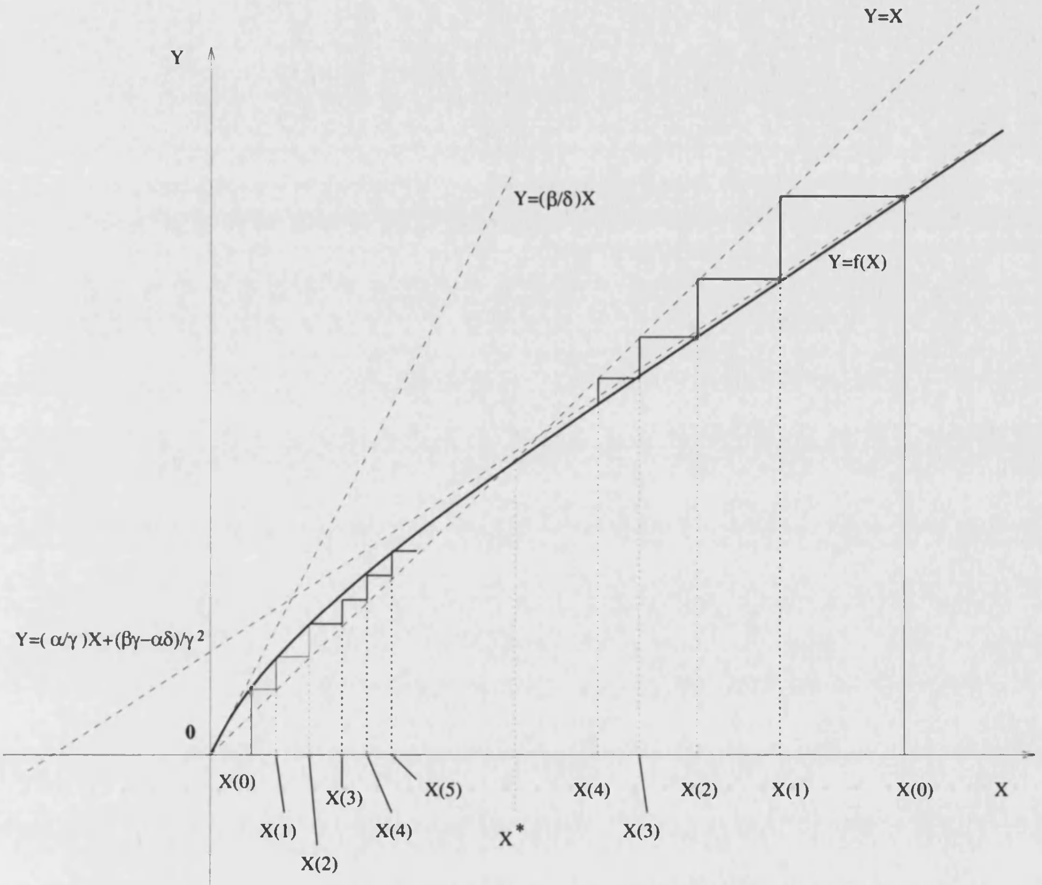

Figure 2.5: Stable coexistence is a possible outcome of the model. In the figure, any initial condition tends to X^* with time. This happens within parameter settings where $\frac{\beta}{\delta} > 1 > \frac{\alpha}{\gamma}$. However, numbers that fulfil these conditions are not biologically realistic.

2.4 Conclusions

When $X(t) \to \infty$ as $t \to \infty$ it is concluded that $N_s(t) \to \infty$ and that therefore $N_a(t) \to 0$. Consequently, fixation of sexual reproduction is obtained, as in case 1a. Analogously, when $X(t) \to 0$ as $t \to \infty$, it can be said that $N_s(t) \to 0$ and $N_a(t) \to \infty$ and concluded that asexuals go to fixation (case 1c). Behind these concluding remarks is the implicit assumption that both sexual and asexual individuals are equally affected by the environment, not that any of these populations can actually grow indefinitely. If such were the case, $X(t) \to \infty$ or $X(t) \to 0$ would not give relevant information. A quotient of two potentially infinite quantities may go to infinity without the denominator going to zero, but only increasing much more slowly than the numerator. However, since the interest is in following the evolution of numbers N_s and N_a, the environmental restriction need not be made explicit in the formulas. A modification of the model to introduce environmental restrictions has been discussed at the beginning of the analysis. It was seen that results would still be the same and thus these conclusions would be valid.

The model developed and its results show that there is not a possibility for the coexistence of sexual and asexual reproduction when only temporal dynamics of a population mixed for reproductive mode are considered. This model is based on a careful revision of the different aspects of the evolution of asexual reproduction in flowering plants as a result of a mutation. It has included every aspect of this question that is essential to understand the costs and advantages of such an evolutionary strategy. It has also revised the way such aspects have been incorporated in previous models dealing with the subject. Just as those models, this model cannot explain the coexistence of sexual and asexual conspecific plants observed in the field. The only case where a polymorphic stable steady state was found has been shown to make no sense in terms of the parameters of the model. That is, such a stable polymorphic steady state is not biologically realistic.

Therefore, the research is compelled to develop other kind of models that include the spatial distribution of individuals in populations mixed for reproductive mode. This new line of work has been pointed out by Mogie (1992), recalled by Joshi and Moody (1995, 1998), although they have developed no spatial model for the cost of sex and, finally, explored by Britton and Mogie (2001). They first approach to this new problem is by means of a reaction-diffusion equation which cannot justify the existence of a polymorphic steady state. However, they also bring to attention the fact that diffusion may not be a realistic way of modelling the dispersal of a sexual/asexual propagule into a population dominated by individuals of the other morph.

It is necessary to realistically incorporate the patterns of pollen and seed dispersal. Pollen exchange, for instance, is usually between close neighbours (Bertin, 1988). A plant is visited by a small number of pollen donors (Meagher, 1986). This could give rise to a series of subpopulations of individuals sharing a certain reproductive mode. The question to investigate is whether such centres would disperse or die away since they are surrounded by neighbouring plants with another reproductive mode. In terms of pollen recruitment, the reproductive mode of a propagule initiating one of these centres of invasion would be more relevant in a spatial model than in models where only temporal dynamics are considered. However, before moving into diffusion models, other approaches will be investigated.

Appendix: A rigorous justification of the dynamics argument

Referring back to the first case, recall that there $\beta\gamma - \alpha\delta < 0$, and that there were three different subcases, namely case 1a, $1 < \frac{\beta}{\gamma} < \frac{\alpha}{\delta}$, where X_t tends to infinity; case 1b, $\frac{\beta}{\gamma} < 1 < \frac{\alpha}{\delta}$, where X^* is an unstable steady state; and case 1c, $\frac{\beta}{\gamma} < \frac{\alpha}{\delta} < 1$, where X_t tends to zero.

Proposition 3.1. If $1 < \frac{\beta}{\delta} < \frac{\alpha}{\gamma}$, then X_t is an increasing unbounded sequence.

Proof. The argument makes use of mathematical induction as follows:

(i) The base of the induction argument is as follows:

$$\frac{X_1}{X_0} > 1$$

$$\Leftrightarrow \alpha X_0 + \beta > \gamma X_0 + \delta$$

$$\Leftrightarrow (\alpha - \gamma)X_0 > \delta - \beta$$

$$\Leftrightarrow X_0 > \frac{\delta - \beta}{\alpha - \gamma},$$

which is true since the number $\frac{\delta-\beta}{\alpha-\gamma}$ is negative. Therefore, the sequence X_t increases from X_0 to X_1, which constitutes the basis of the induction argument.

(ii) Assume now that the increasing relation holds for any two consecutive terms and try to prove that it will be so for subsequent terms. For the purpose of implementing this strategy, notice that the function

$$g(X) := \frac{f(X)}{X} = \frac{\alpha X + \beta}{\gamma X + \delta}$$

is increasing in case 1, since $\beta\gamma - \alpha\delta < 0$ and $g'(X) = \frac{\alpha\delta - \beta\gamma}{(\gamma X + \delta)^2}$. Proceeding with the proof, let $\frac{X_t}{X_{t-1}} > 1$. Then, due to the monotonicity of g, the following relations hold

$$\frac{X_{t+1}}{X_t} = \frac{\alpha X_t + \beta}{\gamma X_t + \delta} = g(X_t) > g(X_{t-1}) = \frac{\alpha X_{t-1} + \beta}{\gamma X_{t-1} + \delta} = \frac{X_t}{X_{t-1}} > 1.$$

It has thus been proved that X_t is increasing. It will now be shown, by contradiction, that it is unbounded. Let us assume that the sequence X_t has a finite limit L. Then, passing to the limit in both sides of the formula (*cf.* (2.4)) $X_{t+1} = \frac{(\alpha X_t + \beta)X_t}{\gamma X_t + \delta}$ as $n \to \infty$, the following equation on L is obtained

$$L = \frac{\alpha L + \beta}{\gamma L + \delta} L$$

$$\Leftrightarrow 1 = \frac{\alpha L + \beta}{\gamma L + \delta}$$

$$\Leftrightarrow L = \frac{\delta - \beta}{\alpha - \gamma} < 0.$$

This is a contradiction since the positive sequence X_t cannot have a negative limit. Therefore, X_t tends to infinity.

It has thus been proved that X_t is a strictly increasing sequence that tends to infinity. ■

Proposition 3.2. If $\frac{\beta}{\delta} < 1 < \frac{\alpha}{\gamma}$, then X^* is an unstable steady state of the sequence X_t. Moreover, if the initial value X_0 is less than X^*, then $X_t \to 0$ as $n \to \infty$; if X_0 is greater than X^*, then $X_t \to \infty$ as $n \to \infty$.

Proof. It will now be proved that X_t is strictly decreasing for any initial condition below X^*. The induction argument to show this runs as follows:

(i) Assume that $X_0 < X^* = \frac{\delta - \beta}{\alpha - \gamma}$. Then

$$(\alpha - \gamma)X_0 < \delta - \beta$$

$$\Leftrightarrow \alpha X_0 + \beta < \gamma X_0 + \delta$$

$$\Leftrightarrow \frac{\alpha X_0 + \beta}{\gamma X_0 + \delta} < 1$$

$$\Leftrightarrow X_0 > X_1.$$

(ii) Next suppose that $\frac{X_t}{X_{t-1}} < 1$. Then, because g is an increasing function, the following relations hold

$$\frac{X_{t+1}}{X_t} = \frac{\alpha X_t + \beta}{\gamma X_t + \delta} = g(X_t) < g(X_{t-1}) = \frac{\alpha X_{t-1} + \beta}{\gamma X_{t-1} + \delta} = \frac{X_t}{X_{t-1}} < 1.$$

This proves that the sequence X_t is strictly decreasing if the initial condition is below X^*. It will be shown that in addition to this the limit L of the sequence is 0. Indeed, passing to the limit as $n \to \infty$ in the formula (*cf.* (2.4)) $X_{t+1} = \frac{(\alpha X_t + \beta)X_t}{\gamma X_t + \delta}$, then the equation $L = \frac{(\alpha L + \beta)L}{\gamma L + \delta}$ is obtained. Since, clearly, $\frac{\alpha L + \beta}{\gamma L + \delta} > 0$, it is possible to conclude that $L = 0$. In particular, this means that $N_s(t) \to 0$ as $t \to \infty$.

Now the behaviour of X_t when the initial condition is above the value X^* will be investigated. To this end, an induction argument will be used again:

(i) Let it be assumed that $X_0 > X^* = \frac{\delta - \beta}{\alpha - \gamma}$. Then

$$(\alpha - \gamma)X_0 > \delta - \beta$$

$$\Leftrightarrow \alpha X_0 + \beta > \gamma X_0 + \delta$$
$$\Leftrightarrow \frac{\alpha X_0 + \beta}{\gamma X_0 + \delta} > 1$$
$$\Leftrightarrow X_0 < X_1.$$

(ii) For the next induction step, once again suppose that the inequality $\frac{X_t}{X_{t-1}} > 1$ holds and prove the inequality $\frac{X_{t+1}}{X_t} > 1$, as follows:

$$\frac{X_{t+1}}{X_t} = \frac{\alpha X_t + \beta}{\gamma X_t + \delta} = g(X_t) > g(X_{t-1}) = \frac{\alpha X_{t-1} + \beta}{\gamma X_{t-1} + \delta} = \frac{X_t}{X_{t-1}} > 1.$$

Therefore, X_t is increasing when $X_0 > X^*$. As in proposition 3.1, if the sequence had a finite limit L, it would be a negative number. That would be a contradiction and so it can be concluded that it goes to infinity as $n \to \infty$.

Therefore X_t is strictly increasing and unbounded when $X^* < X_0$ and the sequence gets away from X^* once more so that $N_a(t) \to 0$ as $t \to \infty$.

In particular, it has been proved that X^* is an unstable steady state. ■

Proposition 3.3. If $\frac{\beta}{\delta} < \frac{\alpha}{\gamma} < 1$, then X_t is a strictly decreasing sequence and it tends to 0 as $n \to \infty$.

Proof. We proceed as before, with mathematical induction.

(i) First, as the basis of the induction argument, assume that $X_1 < X_0$. Then

$$\frac{X_1}{X_0} < 1$$

$$\Leftrightarrow \alpha X_0 + \beta < \gamma X_0 + \delta$$

$$\Leftrightarrow (\alpha - \gamma)X_0 < \delta - \beta$$

$$\Leftrightarrow X_0 > \frac{\delta - \beta}{\alpha - \gamma},$$

which is true since the value $\frac{\delta-\beta}{\alpha-\gamma}$ is negative.

(ii) If it is assumed that $\frac{X_t}{X_{t-1}} < 1$, then it must be shown that $\frac{X_{t+1}}{X_t} < 1$. This is so because

$$\frac{X_{t+1}}{X_t} = \frac{\alpha X_t + \beta}{\gamma X_t + \delta} = g(X_t) < g(X_{t-1}) = \frac{\alpha X_{t-1} + \beta}{\gamma X_{t-1} + \delta} = \frac{X_t}{X_{t-1}} < 1.$$

The previous argument has proved that X_t is strictly decreasing. In a manner similar to that of the proof of proposition 3.2, one can show that the limit of X_t is 0, which means N_s also tends to 0. ■

The proof for the other cases is very similar to what has been written so far. There is only one case that is worthwhile to explore. That is the case where a stable steady state is found.

Proposition 3.4. If $\frac{\beta}{\delta} > 1 > \frac{\alpha}{\gamma}$, then for every initial condition X_0 such that $X_0 < X^*$, the sequence X_t is strictly increasing and its limit is X^*. Moreover, for any initial condition X_0 such that $X_0 > X^*$, the sequence X_t is strictly decreasing and tends to X^*. Therefore, X^* is a stable steady state.

Proof. It will first be shown that any initial condition X_0 less than X^* makes the system approach precisely the value X^*.

(i) Let X_0 be an initial condition such that $X_0 < X^*$. Then

$$X_0 < X^* = \frac{\delta - \beta}{\alpha - \gamma}$$

$$\Leftrightarrow (\alpha - \gamma)X_0 > \delta - \beta$$

$$\Leftrightarrow \alpha X_0 + \beta > \gamma X_0 + \delta$$

$$\Leftrightarrow \frac{\alpha X_0 + \beta}{\gamma X_0 + \delta} > 1$$

$$\Leftrightarrow X_0 < X_1.$$

Also, it should be observed that

$$X_1 < f(X^*). \tag{2.13}$$

To this end, notice that since in the case under consideration $\beta\gamma - \alpha\delta > 0$, the derivative of the function f, which is given by the formula (*cf.* (2.6)) $f'(X) = \frac{\alpha}{\gamma} + \frac{\delta}{\gamma^3}(\beta\gamma - \alpha\delta)\left(X + \frac{\delta}{\gamma}\right)^{-2}$, is not less than $\frac{\alpha}{\gamma}$, and thus it is positive. Therefore, $f(X_0) < f(X^*) = X^*$, which proves (2.13).

(ii) Since it has been shown that X_1 increases with respect to X_0, it can now be assumed that the same happens for any two arbitrary consecutive terms of X_t. That is, it is assumed that $X_t > X_{t-1}$. Moreover, it is assumed that $X_t < X^*$. It must now be shown that $X_{t+1} > X_t$ and that $X_{t+1} < X^*$. Hence, using the monotonicity of the function f shown above, one gets

$$X_{t+1} = \frac{(\alpha X_t + \beta)X_t}{\gamma X_t + \delta} = f(X_t) > f(X_{t-1}) = \frac{(\alpha X_{t-1} + \beta)X_{t-1}}{\gamma X_{t-1} + \delta} = X_t.$$

Moreover, X_{t+1} will not go beyond X^* because $X_t < X^*$, and thus, again due to the monotonicity of the function f, the relations $f(X_t) < f(X^*) = X^*$ are satisfied. This proves that the sequence monotonically tends to X^* from below, if the initial condition is below this value.

On the other hand, for an initial condition X_0 such that $X_0 > X^*$ it is easy to see that

(i) $X_0 > X_1$ because

$$\begin{aligned} &(\alpha - \gamma)X_0 < \delta - \beta \\ \Leftrightarrow\ &\alpha X_0 + \beta < \gamma X_0 + \delta \\ \Leftrightarrow\ &\frac{\alpha X_0 + \beta}{\gamma X_0 + \delta} < 1 \\ \Leftrightarrow\ &X_0 > X_1. \end{aligned}$$

Also, $X_1 = f(X_0) > f(X^*) = X^*$.

(ii) Assume that the same relation holds for two arbitrary terms of the sequence X_t, that is, $X_t < X_{t-1}$, and that $X_t > X^*$. Then the following relations hold:

$$X_{t+1} = \frac{(\alpha X_t + \beta)X_t}{\gamma X_t + \delta} = f(X_t) < f(X_{t-1}) = \frac{(\alpha X_{t-1} + \beta)X_{t-1}}{\gamma X_{t-1} + \delta} = X_t.$$

Further, $X_{t+1} = f(X_t) > f(X^*) = X^*$, which concludes the induction step. It has thus been proved that X_t monotonically tends to X^* from above, if the initial condition is above this value.

This constitutes the proof of the fact that X^* is a stable steady state. ■

Chapter 3

Sexuality *vs.* Asexuality: Implicit Introduction of Space with a Patch-occupancy Model

In the chapter that presented the biological context of this work, it was seen that the coexistence of sexual and asexual relatives proposes an interesting line of research. The problem derives from an old discussion among evolutionary biologists about the evolution and maintenance of sexual reproduction. Considered a costly way of reproduction, it is difficult to understand why the sexual variant evolved in the first place and how it has maintained itself in spite of asexual reproduction. Particularly in those species where it is clear that extant asexual forms are descended from sexual ancestors, the existence of mixed populations seems contradictory. Thus, one question that can be posed regarding the coexistence of sexual and asexual conspecifics is whether such coexistence is real or is due to niche differentiation in a heterogeneous environment. It was further discussed how mathematical models on this subject have failed to capture this well-documented phenomenon (*e.g.* the coexistence of sexual and asexual reproduction in populations of the common dandelion *Taraxacum officinale*) unless they invoke external factors, such as the presence of parasites (Hamilton *et al.*, 1990; Keeling and Rand, 1995). The geographic distribution of sexual and asexual forms, with the former reigning towards the tropics, while the latter are more common in the harsher environments found at higher altitudes and latitudes, and with regions of overlap in the centre of these distributions, has also suggested that the coexistence of sexual and asexual forms could be only a phase of an evolutionary process that would end in the spatial separation of these forms. Such a process would be slow, since the total spatial differentiation of sexual and asexual relatives may not be observed within an interglacial period (*circa* 15,000 years, see Forsstrom, 2001). Finally, it was suggested that mathematical models that include spatial aspects of the coexistence of sexual and asexual relatives could help towards a better understanding of this situation.

In order to start the study of the spatial dynamics of sexuality *vs.* asexuality, the metapopulation concept (Levins, 1970) will be used. *A grosso modo*, a metapopulation is a population of populations, spatially separated but linked by migration (Hanski, 1999; van Baalen, 2000). The metapopulation approach is the most straightforward way to introduce space into a model, although this introduction is implicit. Because the dynamics of the array of subpopulations, or patches, is reduced to a set of equations in the proportion of patches in each state (*e.g.* presence/absence of species in a given patch), this kind of model cannot include the effects of the spatial arrangement of the patches (Caswell and Etter, 1993). Thus, there is a notion of space involved, but no actual spatial structure (Hiebeler, 1997). Moreover, all patches are equally accessible, *e.g.* for colonisation, regardless of their locations. This aspect also makes of metapopulation models an implicit spatial approach (Neuhauser, 2001). There are many examples where metapopulation models have been useful to explain phenomena that otherwise seemed contradictory when modelled with a traditional approach, *e.g.* coexistence of competing species and persistence of fugitive species (Hastings, 1980; Barradas and Cohen, 1994). The author of this thesis has studied an extension of the Barradas and Cohen model (Carrillo, 1997). In that study, evidence was found that, in a metapopulation model, environmental disturbances may provide a respite to the weaker competitor, which is eliminated locally by the stronger competitor but persists at a global scale, and thus promote the overall coexistence of species.

A metapopulation approach to the coexistence of sexual and asexual conspecifics could place a population over an infinite number of discrete patches that can be occupied by either sexual or asexual individuals. This would enable the model to study the evolution in time of the fraction of patches that are occupied by sexual/asexual individuals and investigate if at some point both these numbers will be different from zero. Strictly speaking, a particular case of a metapopulation would be used as only one individual would occupy a patch. Although one individual could be considered a subpopulation of genes, and the genetic exchange between individuals could be considered analogous to migration between the subpopulations comprising this 'genetic metapopulation', the emphasis of this work is not on population genetics but on ecology. The individual-based approach that is going to be used in this first spatial model corresponds to what has been defined as patch-occupancy models (Caswell and Etter, 1993). This approach also permits the inclusion of empty patches. These would constitute territory open to colonisation by the propagules of sexual and asexual individuals. Thus, dispersal would also be considered. These empty patches would be created by the natural death of mature individuals that occupy a patch, or by the action of disturbances on the habitat of the population. Should these disturbances have an effect on a patch, it would result in the removal of the individual holding it and the appearance of a new space for colonisation. This last process, colonisation, is of importance as in some works asexuals are considered better colonisers. This could increase the advantages of asexuals and the costs for sexuals. However, empty spaces could also be the way in which, via dispersal of propagules, sexuals may invade new territory and persist (Mogie, 1992).

Patch-occupancy models have also proved useful when considering the interaction of individuals with their environment. No habitat is forever stable. Disturbances play a very important role in the dynamics of a population. For instance, species richness of intertidal ecosystems has been shown to reach a maximum under the action of disturbances at intermediate frequencies (Dayton and Hessler, 1972; Connell, 1978; Chesson, 1985). The influence of environmental disturbances on species diversity in an ecosystem has been extensively modelled and discussed by Caswell and Cohen (1991a, 1991b, 1993). Within the biological context of this thesis, sexual and asexual individuals do not have the same fitness with respect to any habitat where they seem to be coexisting. As far as the inclusion of environmental disturbances is concerned, it could reflect the different viabilities of sexually and asexually derived offspring. Genetic recombination has been considered as one advantage of sexual reproduction (Greenwood and Adams, 1987; Stearns, 1987; Michod and Levin, 1988; Mogie, 1992) because when facing the threats posed by the environment, such as diseases or temperature changes, a species represented by a wide diversity of genotypes would be more likely to survive. If asexuality is more linked to the massive replication of a few genotypes, it is plausible to think that they may be more susceptible to a disturbance affecting those particular genotypes in the habitat. Environmental disturbances could be built into the model in such a way that they reflect these observations.

3.1 The patch-occupancy model

Hopefully, the preceding arguments will have justified the potential usefulness of a patch-occupancy approach to the problem of sexual *vs.* asexual reproduction. The model will be presented and discussed in the following sections.

3.1.1 Assumptions of the model and notation

The environment is a collection of an infinite number of identical patches where one species is present. This landscape is occupied by a species of flowering plant. Within this species some individuals exhibit sexual reproduction and will be referred to as sexuals. Other individuals reproduce asexually, producing eggs that do not require fertilisation to develop into mature individuals. They will be known as asexuals.

Each patch in this habitat can either be empty, occupied by a sexual individual or occupied by an asexual individual. The symbols p_s, p_a and p_0 will denote the fractions of patches in the habitat that are occupied by sexuals, asexuals or are empty, respectively. Attention will be paid to two processes: colonisation of empty patches and persistence of individuals in the patches they occupy. Propagules of sexuals and asexuals colonise empty patches. They do it randomly and without neighbour effects or advantages. However, it is not implied that the dispersal of sexual and asexual propagules is the same. Dispersal coefficients of sexuals and asexuals may differ due to the characteristics of the seeds they produce. Moreover, the number of propagules reaching an empty patch is assumed to be directly proportional to the number of occupied patches. This should reflect morph differentiation. Thus, there are different colonisation rates for each reproductive mode. These colonisation rates are given by a Poisson distribution. The probability that a sexual propagule reaches an empty patch is given by $C_s = 1 - \mathrm{e}^{-d_s p_s}$, where d_s is the dispersal coefficient of sexuals. Analogously, the probability that an asexual propagule reaches an empty patch is given by $C_a = 1 - \mathrm{e}^{-d_a p_a}$, where d_a is the dispersal coefficient of asexuals. Under the action of a disturbance, colonisation is not possible. In the event that an empty patch is to be colonised by a sexual and an asexual at the same time, asexuals prove to be better colonisers and get hold of the empty patch, displacing sexuals. This is the only inter-morph interaction considered in the model so far.

An occupied patch becomes available for colonisation only following the death of its occupant. Death may be natural or due to the action of disturbances, which do not affect sexual and asexual individuals in the same way, but do have consequences on the colonisation and persistence of both. However, disturbances have the same intensity over the whole landscape. That is, they occur independently and are equal for all patches. For simplicity, they are also considered to be constant in time. Regardless of its causes, removal of individuals from the landscape will be summarised in one term: the probability that an occupied patch becomes empty. Morph differentiation is also reflected here. Thus, the probability that a patch occupied by a sexual individual becomes empty will be denoted by σ, $0 \leq \sigma \leq 1$. Analogously, the probability that a patch occupied by an asexual individual becomes empty will be denoted by α, $0 \leq \alpha \leq 1$.

3.1.2 Mathematical framework

The general state of the landscape at any given moment is described by $\mathbf{p}(t) \in \mathbb{R}^3$, $\mathbf{p}(t) = (p_0(t), p_s(t), p_a(t))$, where $p_0(t)$ is the fraction of empty patches, $p_s(t)$ is the fraction of patches occupied by sexuals and $p_a(t)$ is the fraction of patches occupied by asexuals at time t. The dynamics of this system, that is, the change from one unit of time to the next, will be described by a nonlinear Markov chain

$$\mathbf{p}(t+1) = A(\mathbf{p}(t))\mathbf{p}(t),$$

where $A(\mathbf{p}(t))$ is the transition matrix given by

$$\begin{pmatrix} 1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha) & \sigma & \alpha \\ C_s(1-\sigma)(1-C_a) & 1-\sigma & 0 \\ C_a(1-\alpha) & 0 & 1-\alpha \end{pmatrix}.$$

This transition matrix $A(\mathbf{p}(t))$ is derived from the assumptions about the processes of persistence and colonisation. Take, for instance, A_{s0}, the entry that describes the probability of an empty patch at time t becoming occupied by a sexual at time $t+1$. This event takes place if a sexual propagule reaches an empty patch, the corresponding probability being C_s, and if disturbances do not prevent colonisation by sexuals from taking place, the probability being $1-\sigma$. Also, it is required that no asexual propagule is trying to colonise the same patch. That happens with probability $1 - C_a$. All these requirements together give the entry $A_{s0} = C_s(1-\sigma)(1-C_a)$. All other entries of the transition matrix are worked out in an analogous manner. In general, an entry A_{ij} describes the probability of a patch in state j at time t changing to state i at time $t+1$, where $i, j = 0, s, a$.

Thus, the following system is obtained:

$$\begin{pmatrix} p_0(t+1) \\ p_s(t+1) \\ p_a(t+1) \end{pmatrix} = \begin{pmatrix} 1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha) & \sigma & \alpha \\ C_s(1-\sigma)(1-C_a) & 1-\sigma & 0 \\ C_a(1-\alpha) & 0 & 1-\alpha \end{pmatrix}$$

$$\times \begin{pmatrix} p_0(t) \\ p_s(t) \\ p_a(t) \end{pmatrix}. \tag{3.1}$$

The processes described by this system may be split into a dispersal phase given by

$$\begin{aligned} p_s^{disp} &= p_s(t) + C_s(1-C_a)p_0(t), \\ p_a^{disp} &= p_a(t) + C_a p_0(t), \end{aligned}$$

and a disturbance phase given by

$$\begin{aligned} p_s(t+1) &= (1-\sigma)p_s^{disp}, \\ p_a(t+1) &= (1-\alpha)p_a^{disp}, \end{aligned}$$

in such a way that (*cf.* (3.1))

$$\begin{aligned} p_s(t+1) &= (1-\sigma)p_s(t) + C_s(1-C_a)(1-\sigma)p_0(t), \\ p_a(t+1) &= (1-\alpha)p_a(t) + C_a(1-\alpha)p_0(t). \end{aligned}$$

3.1.3 Mathematical analysis of the model with a first-order approximation to the Poisson colonisation process

Once the mathematical framework has been set, it is possible to show that this mathematical treatment is consistent in biological terms. That is, starting from a given landscape composition $\mathbf{p}(t)$, the proposed transformation will map it onto another composition of the landscape $\mathbf{p}(t+1)$. In mathematical terms, it will be shown that the set of all possible landscape configurations, denoted by Ω, is invariant under the action of the matrix $A(\mathbf{p}(t))$. This will be done in the appendix to this chapter.

Knowing that the model is consistent, work must proceed to investigate its behaviour. In what follows, the equilibrium points of the system (3.1) will be obtained, together with the conditions for their existence and stability. The fixed points of the system are found when the condition $\mathbf{p}(t+1) = \mathbf{p}(t)$ is satisfied.

That is, when the following equalities hold simultaneously

$$(1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha) - 1)p_0(t) + \sigma p_s(t) + \alpha p_a(t) = 0,$$

$$C_s(1-\sigma)(1-C_a)p_0(t) + ((1-\sigma) - 1)p_s(t) = 0$$

and

$$C_a(1-\alpha)p_0(t) + ((1-\alpha) - 1)p_a(t) = 0.$$

Since $p_0(t) + p_s(t) + p_a(t) = 1$, substitution of $p_0(t)$ by $1 - p_s(t) - p_a(t)$ in the formulas above is possible. Work on the original system is thus reduced to only the following two equations in the variables p_s and p_a:

$$C_s(1-\sigma)(1-C_a)(1-p_s-p_a) - \sigma p_s = 0 \tag{3.2}$$

and

$$C_a(1-\alpha)(1-p_s-p_a) - \alpha p_a = 0. \tag{3.3}$$

Notice that the expression on the left-hand side (LHS) of (3.2)

$$\Delta p_s := C_s(1-\sigma)(1-C_a)(1-p_s-p_a) - \sigma p_s \tag{3.4}$$

describes the changes in the fraction of patches occupied by sexual individuals from one unit of time to the next, while the LHS of (3.3)

$$\Delta p_a := C_a(1-\alpha)(1-p_s-p_a) - \alpha p_a \tag{3.5}$$

describes those changes for the fraction of patches occupied by asexuals. When both equations (3.2) and (3.3) hold, these fractions are no longer changing and the system has reached an equilibrium state.

The equations that describe the fraction of patches occupied by sexuals or asexuals at time $t+1$ in terms of the values of these fractions at time t are given by

$$\begin{aligned} p_s(t+1) &= f(p_s(t), p_a(t)) \\ &= C_s(1-\sigma)(1-C_a)(1-p_s(t)-p_a(t)) + (1-\sigma)p_s(t) \end{aligned} \tag{3.6}$$

and

$$p_a(t+1) = g(p_s(t), p_a(t)) = C_a(1-\alpha)(1-p_s(t)-p_a(t)) + (1-\alpha)p_a(t). \tag{3.7}$$

These equations are nonlinear. In particular, they include transcendental terms. It is difficult to give precise expressions for the fixed points of this system. However, understanding of the system can be gained by using a uniform, rather than Poisson, distribution of propagules. This can be done by considering the well-known approximations $1 - \mathrm{e}^{-d_s p_s} \approx d_s p_s$ and $1 - \mathrm{e}^{-d_a p_a} \approx d_a p_a$ to the originally proposed Poisson process. These approximations are valid for sufficiently small p_s and p_a. Moreover, using the Lagrange formula for the remainder, an exact expression for the error of these approximations, $|1 - \mathrm{e}^{-d_i p_i} - d_i p_i|$, where $i = s,\ a$, can be obtained. Namely, $|1 - \mathrm{e}^{-d_i p_i} - d_i p_i| = \frac{1}{2} d_i^2 p_i^2$. To keep this error within a certain percentage ϵ of the approximation $d_i p_i$, that is, to make $\frac{1}{2} d_i^2 p_i^2 < \epsilon d_i p_i$, it suffices to make $p_s < \frac{2\epsilon}{d_s}$. Notice that the dispersal coefficient d_i also has an influence on the accuracy of the approximation. Using the proposed approximations, the system (3.6)–(3.7) then becomes

$$\begin{aligned} p_s(t+1) &= d_s p_s(t)(1 - d_a p_a(t))(1-\sigma)(1 - p_s(t) - p_a(t)) + (1-\sigma) p_s(t), \\ p_a(t+1) &= d_a p_a(t)(1-\alpha)(1 - p_s(t) - p_a(t)) + (1-\alpha) p_a(t), \end{aligned} \tag{3.8}$$

while the homogeneous system whose solutions are the equilibria of (3.8) is now

$$\begin{aligned} \Delta p_s &= d_s p_s (1 - d_a p_a)(1-\sigma)(1 - p_s - p_a) - \sigma p_s = 0, \\ \Delta p_a &= d_a p_a (1-\alpha)(1 - p_s - p_a) - \alpha p_a = 0. \end{aligned}$$

These systems are also nonlinear, but they involve no transcendental terms. They can be handled using standard techniques for the analysis of a system of two nonlinear difference equations, as will be done next.

The zeroclines for Δp_s are given by

$$p_s = 0 \tag{3.9}$$

and

$$(1 - d_a p_a)(1 - p_s - p_a) = \frac{\sigma}{d_s(1-\sigma)}. \tag{3.10}$$

The corresponding zeroclines for Δp_a are

$$p_a = 0 \tag{3.11}$$

and

$$p_a + p_s = 1 - \frac{\alpha}{(1-\alpha)d_a}. \tag{3.12}$$

It will be seen that the values of the numbers $\mathcal{S} := \frac{\sigma}{d_s(1-\sigma)}$ and $\mathcal{A} := \frac{\alpha}{d_a(1-\alpha)}$ are determinant in the number and quality of the steady states the system will exhibit. These numbers will play an important role in the discussion that follows. They are, in fact, less arbitrary than one may think and have clear biological interpretations. Consider the basic reproductive rate

$$\text{Basic Reproductive Rate} = \frac{\text{colonisation rate}}{\text{mortality rate}}.$$

It can immediately be seen that $\mathcal{S}$ and $\mathcal{A}$ are the inverse of the BRR for sexuals and asexuals, respectively. It is in terms of these numbers that the study of the steady states of the system will be made.

In general, the steady states are given by the intersection of zeroclines, as shown in figure 3.1. The point where the zeroclines (3.9) and (3.11) meet, which is $(0,0)$ in the $p_s - p_a$ plane, always exists as an element of $\omega = [0,1] \times [0,1]$, but the behaviour around it is different according to different cases. At the point $(0,0)$ all patches are empty. This point is $(1,0,0)$ in the original $p_0 - p_s - p_a$ system. The intersection of the zeroclines (3.10) and (3.11) represents the purely sexual steady state of the system. That is, a state where a fraction of patches is occupied by sexuals and the rest are empty, denoted $(p_s^*, 0)$ in the $p_s - p_a$ plane or $(1-p_s^*, p_s^*, 0)$ in the $p_0 - p_s - p_a$ space. The intersection of the zeroclines (3.9) and (3.12) accounts for the purely asexual steady state $(0, p_a^*)$ in the $p_s - p_a$ plane or $(p_a^*, 0, 1-p_a^*)$ in the $p_0 - p_s - p_a$ space. Finally, the intersection of the zeroclines (3.10) and (3.12) will be the coexistence steady state $(\hat{p}_s, \hat{p}_a)$ in the $p_s - p_a$ plane or $(1 - \hat{p}_s - \hat{p}_a, \hat{p}_s, \hat{p}_a)$ in the $p_0 - p_s - p_a$ space. At this point, both sexual and asexual individuals are present in the landscape.

Applying the previous general discussion to the problem, notice that the steady states of the system (3.8) are the following: (i) $(0,0)$; (ii) $(1-\mathcal{S}, 0)$; (iii) $(0, 1-\mathcal{A})$ and (iv) $(1 - \mathcal{A} - \frac{1}{d_a}(1 - \frac{\mathcal{S}}{\mathcal{A}}), \frac{1}{d_a}(1 - \frac{\mathcal{S}}{\mathcal{A}}))$.

The linearisation of the system (3.6)–(3.7) in a neighbourhood of a steady state (p_s^0, p_a^0) is given by

$$\begin{aligned} p_s(t+1) &= p_s^0 + \left.\frac{\partial f(p_s,p_a)}{\partial p_s}\right|_{(p_s^0,p_a^0)} (p_s(t) - p_s^0) + \left.\frac{\partial f(p_s,p_a)}{\partial p_a}\right|_{(p_s^0,p_a^0)} (p_a(t) - p_a^0), \\ p_a(t+1) &= p_a^0 + \left.\frac{\partial g(p_s,p_a)}{\partial p_s}\right|_{(p_s^0,p_a^0)} (p_s(t) - p_s^0) + \left.\frac{\partial g(p_s,p_a)}{\partial p_a}\right|_{(p_s^0,p_a^0)} (p_a(t) - p_a^0). \end{aligned} \tag{3.13}$$

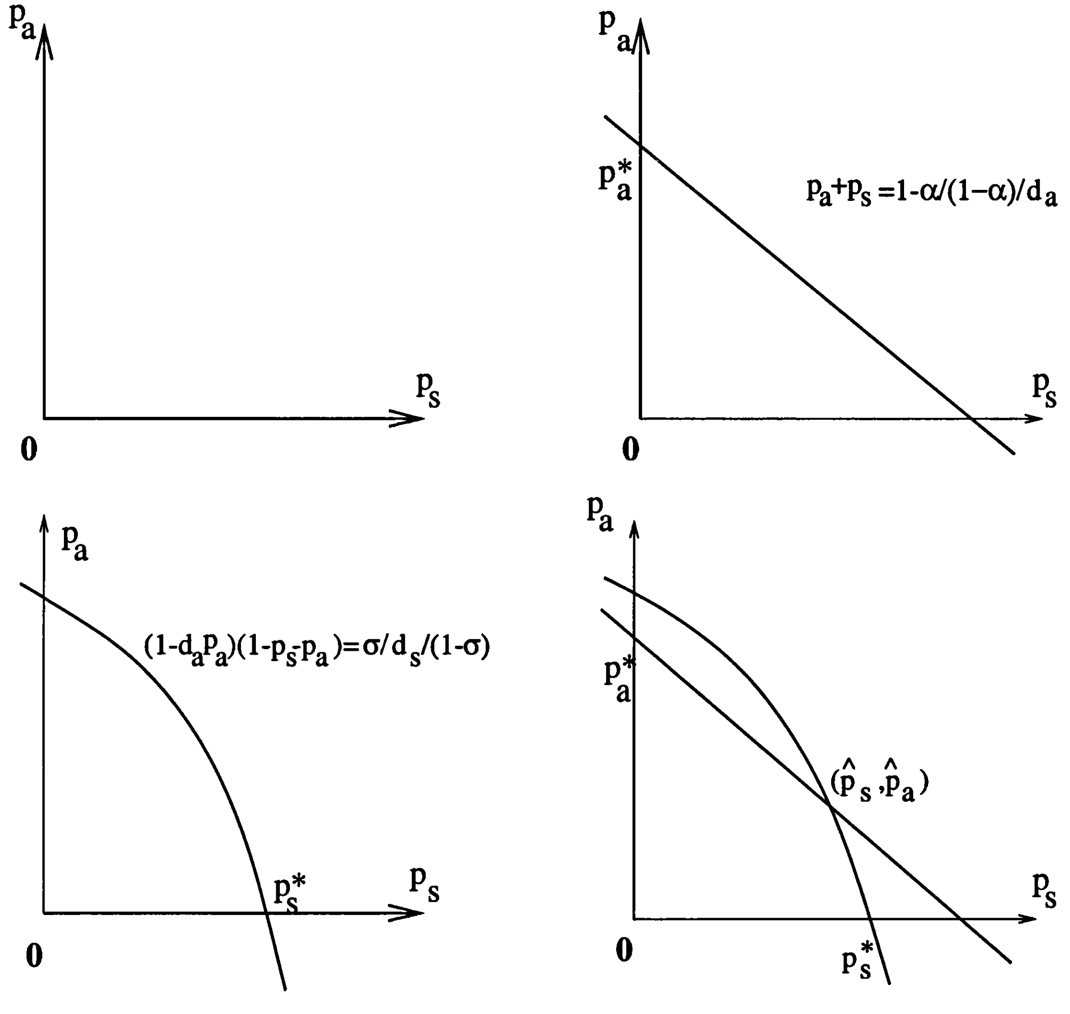

Figure 3.1: The figure shows how the intersection of the different zeroclines determines the steady states of the dynamical system in the patch-occupancy model. $(0,0)$, the trivial steady state, corresponds to exclusion of both types from the landscape; $(p_s^*,0)$ is the semitrivial steady state where only sexuals prevail; $(0,p_a^*)$ is the semitrivial steady state corresponding to dominance of the landscape by asexuals; and $(\hat{p}_s,\hat{p}_a)$ is the coexistence steady state.

The behaviour of the system (3.8) around its steady states will be investigated next. This can be achieved by studying the eigenvalues of the matrix of coefficients in the linearisation (3.13), which are, therefore, the eigenvalues of the Jacobian matrix $\frac{D(f,g)}{D(p_s,p_a)}$ calculated at the point (p_s^0, p_a^0). This matrix will be denoted by

$$J(p_s^0, p_a^0) = \begin{pmatrix} A & B \\ C & D \end{pmatrix},$$

where the components of the matrix are given by the following formulas: $A = d_s(1-\sigma)(1-d_a p_a)(1-2p_s-p_a)+(1-\sigma)$, $B = d_s p_s(1-\sigma)(d_a p_s + 2d_a p_a - 1 - d_a)$, $C = -d_a(1-\alpha)p_a$ and $D = d_a(1-\alpha)(1-p_s-2p_a)+(1-\alpha)$. It is well known that the corresponding eigenvalues are the roots of the characteristic equation

$$\lambda^2 - (A+D)\lambda + (AD - BC) = 0.$$

All four steady states and their corresponding eigenvalues are investigated below.

(i) $(p_s^0, p_a^0) = (0,0)$. Evaluating at this point, the eigenvalues are

$$\lambda_1 = (1-\sigma)(d_s+1)$$

and

$$\lambda_2 = (1-\alpha)(d_a+1).$$

The condition for stability of a steady state is that

$$|\lambda_i| < 1, \quad i = 1,2, \tag{3.14}$$

which in this case means that the inequalities $\frac{1}{\mathcal{S}} < 1$ and $\frac{1}{\mathcal{A}} < 1$ hold. These conditions have a clear biological interpretation. Namely, an empty landscape is the result in this case because, for both sexuals and asexuals, the mortality rate exceeds the colonisations rate when BBR < 1.

(ii) $(p_s^0, p_a^0) = (p_s^*, 0) = (1-\mathcal{S}, 0)$. The eigenvalues that are found when evaluating at this point are

$$\lambda_1 = d_s(1-\sigma)(2\mathcal{S}-1)+(1-\sigma)$$

and

$$\lambda_2 = d_a(1-\alpha)(1-d_a\mathcal{S}).$$

For the purely sexual steady state to be stable, it is required that the conditions

$\mathcal{S} < 1$ and $\frac{\mathcal{S}}{\mathcal{A}} < 1$ are satisfied. In this case, not only is the mortality rate of sexuals less than their colonisation rate, but also their BBR is greater than that of asexuals.

(iii) $(p_s^0, p_a^0) = (0, p_a^*) = (0, 1 - \mathcal{A})$. In this case, the eigenvalues are given by the following formulas:

$$\lambda_1 = d_s(1-\sigma)(1-d_a(1-\mathcal{A}))\mathcal{A} + (1-\sigma)$$

and

$$\lambda_2 = d_a(1-\alpha)(2\mathcal{A}-1) + (1-\alpha).$$

For stability of this steady state where only asexuals prevail, the criteria (3.14) require that $\frac{1}{1-\alpha} - d_a < \frac{\mathcal{S}}{\mathcal{A}}$ and that $\mathcal{A} < 1$. The second condition, $\mathcal{A} < 1$, means that the mortality rate of asexuals does not exceed their colonisation rate, while the first means that their BBR is greater than that of sexuals by a factor $\frac{1-d_a(1-\alpha)}{1-\alpha}$, which represents the colonisation potential of an asexual before it dies.

Finally, (iv) $(p_s^0, p_a^0) = (\hat{p}_s, \hat{p}_a) = (1 - \frac{1}{d_a}(1 - \frac{\mathcal{S}}{\mathcal{A}}) - \mathcal{A}, \frac{1}{d_a}(1 - \frac{\mathcal{S}}{\mathcal{A}}))$. This is the coexistence steady state. The expressions for the corresponding eigenvalues are not as straightforward as those obtained for the previous steady states. However, it will be proved that this steady state is unstable by showing that at least one of the eigenvalues is greater than one. To this end, the difference of the Jacobian matrix $J(\hat{p}_s, \hat{p}_a)$ of the system (3.13) and the identity matrix is considered. The resulting matrix is given by

$$J(\hat{p}_s, \hat{p}_a) - I = \begin{pmatrix} A' & B' \\ C' & D' \end{pmatrix},$$

where $A' = d_s(1-\sigma)(1-d_a p_a)(1-2p_s-p_a) - \sigma$, $B' = d_s p_s(1-\sigma)(d_a p_s + 2d_a p_a - 1 - d_a)$, $C' = -d_a(1-\alpha)p_a$ and $D' = d_a(1-\alpha)(1-p_s-2p_a) - \alpha$.

The following formula for the determinant of this matrix is then obtained

$$\det(J(\hat{p}_s, \hat{p}_a) - I) = -d_s d_a (1-\alpha)(1-\sigma)\mathcal{A}\left(1 - \frac{\mathcal{S}}{\mathcal{A}}\right)\left(1 - \mathcal{A} - \frac{1}{d_a}\left(1 - \frac{\mathcal{S}}{\mathcal{A}}\right)\right),$$

which gives a negative number as long as the point (p_s^0, p_a^0) is in the region of biological interest. Thus, the eigenvalues of the matrix $J(\hat{p}_s, \hat{p}_a) - I$ have different signs and therefore the eigenvalues of $J(\hat{p}_s, \hat{p}_a)$ are separated by 1. Consequently, this steady state is unstable, which makes the coexistence of sexual and asexual forms unlikely.

3.1.4 Mathematical analysis of the original model with Poisson colonisation process

The analysis of the model should now move on to include the original Poisson distribution that describes the dispersal of propagules to empty patches. That is, the analysis will be carried out on equations (3.6) and (3.7), which include transcendental terms that make it difficult to explicitly state expressions for the values of the steady states. This shall be fully appreciated in the discussion that follows.

As before, the way in which the fractions of patches occupied by sexuals and asexuals change from one unit of time to the next is given by the expressions (3.4) and (3.5). Therefore, to find the equilibrium points of this system, it is necessary to simultaneously solve equations (3.2) and (3.3). To this end, in a similar way to what was done before, the expressions for the changes in p_s and p_a will be renamed as

$$\Delta p_s := F(p_s, p_a) = (1 - \mathrm{e}^{-d_s p_s})(1-\sigma)\mathrm{e}^{-d_a p_a}(1 - p_s - p_a) - \sigma p_s,$$

and

$$\Delta p_a := G(p_s, p_a) = (1 - \mathrm{e}^{d_a p_a})(1-\alpha)(1 - p_s - p_a) - \alpha p_a.$$

Then consider the following representation of the function F

$$F(p_s, p_a) = f_1(p_s, p_a) f_2(p_s, p_a)$$

where the terms f_1 and f_2 are given by the formulas

$$f_1(p_s, p_a) := p_s$$

and

$$f_2(p_s, p_a) := \frac{1}{p_s}(1 - \mathrm{e}^{-d_s p_s})(1-\sigma)\mathrm{e}^{-d_a p_a}(1 - p_s - p_a) - \sigma. \tag{3.15}$$

Notice that (3.15) is an analytic function and that $f_2(p_s, p_a) = 0$ makes $\Delta p_s = 0$. The equation $f_2(p_s, p_a) = 0$ implicitly defines a function $p_a(p_s)$ which is one of the zeroclines of interest. The other zerocline is clearly given by the equation $f_1(p_s, p_a) = 0$. Analogously, consider the function G as a product of two more basic expressions

$$G(p_s, p_a) = g_1(p_s, p_a) g_2(p_s, p_a),$$

where

$$g_1(p_s, p_a) := p_a$$

and

$$g_2(p_s, p_a) := \frac{1}{p_a}(1 - \mathrm{e}^{-d_a p_a})(1 - \alpha)(1 - p_s - p_a) - \alpha. \tag{3.16}$$

Once more, notice that the right-hand side of (3.16) is well defined and that the equation $g_2(p_s, p_a) = 0$ implicitly defines a function $\tilde{p}_a(p_s)$ which is one of the zeroclines for Δp_a, while the other is given by $g_1(p_s, p_a) = 0$.

The equilibrium points, and solutions to the homogeneous system (3.2)–(3.3), are found in the intersection of (i) $f_1 = 0$ and $g_1 = 0$; (ii) $f_2 = 0$ and $g_1 = 0$; (iii) $f_1 = 0$ and $g_2 = 0$ and (iv) $f_2 = 0$ and $g_2 = 0$, as shown in figure 3.2. The first point is the trivial steady state $(0, 0)$, where an empty landscape is obtained. This point is, as before, obtained in the most straightforward manner, as it rests at the origin of the $p_s - p_a$ plane. The second point is a semi-trivial steady state $(p_s^*, 0)$, where only sexuals are present in the landscape while the third point, $(0, p_a^*)$ is another semi-trivial steady state where sexuals have disappeared and only asexuals are present in the landscape. Finally, the intersection of the curves $f_2 = 0$ and $g_2 = 0$, if it exists, is the point that marks coexistence of sexual and asexual forms in the population. By analogy to the notation in the previous section, this point will be denoted $(\hat{p}_s, \hat{p}_a)$. In the following, conditions for the existence of this point are discussed. Furthermore, conditions for its stability are set. The same will, of course, be done for all other steady states of the system, including the unstable steady state $(\hat{p}_s, \hat{p}_a)$. To complete these tasks, it is necessary to look more carefully at the non-trivial zeroclines (3.15) and (3.16). A brief note is made here that, although the same notation is used to nominate the steady states, they are not the same as those for the simplified system studied in the previous section.

On the behaviour of the zerocline given by the equation $f_2(p_s, p_a) = 0$

The zerocline $f_2(p_s, p_a) = 0$ implicitly defines a curve $p_a(p_s)$ on the $p_s - p_a$ plane. It is difficult to find out what this curve is precisely, but it is possible to determine the existence and uniqueness of its intersection points with the axes p_s and p_a.

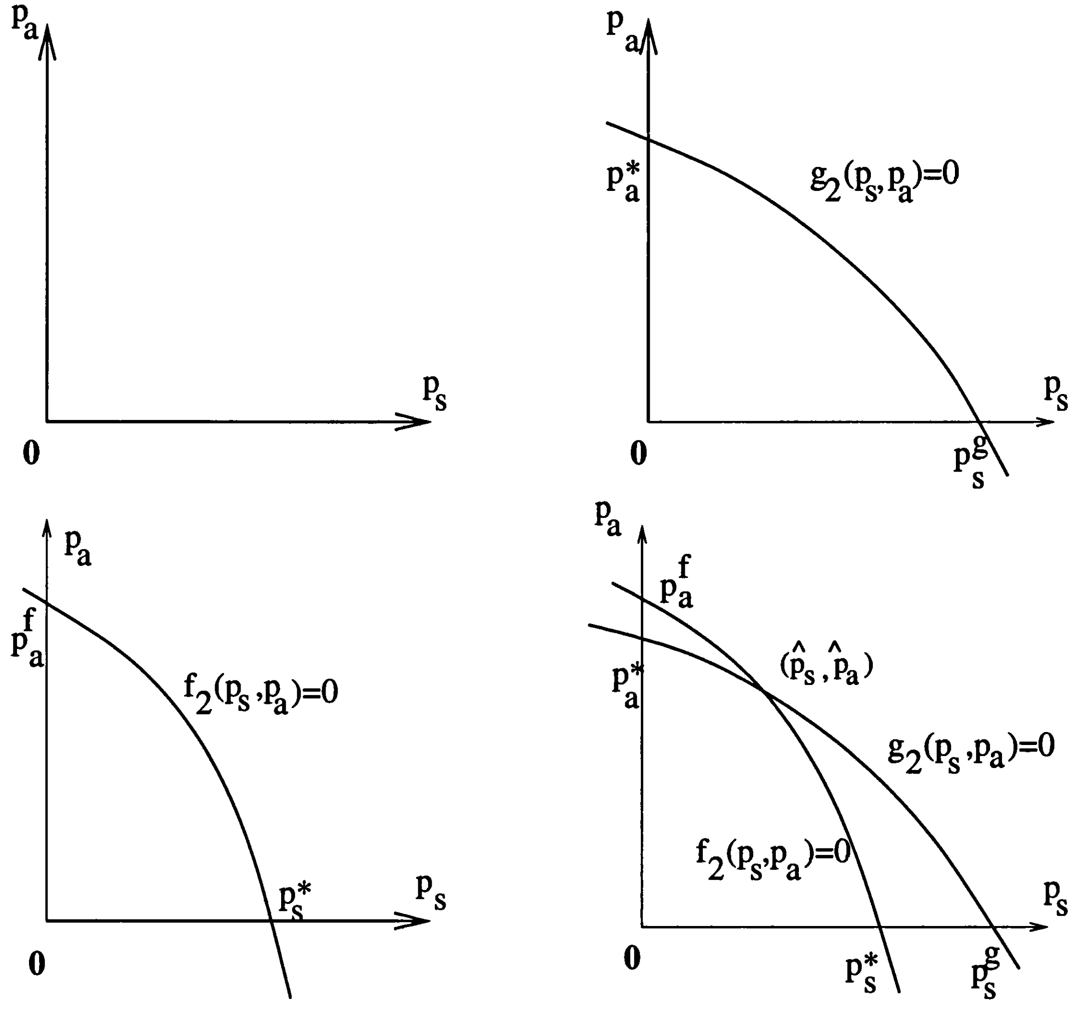

Figure 3.2: The figure shows the intersection of the different zeroclines and the steady states of the dynamical system they determine in the patch-occupancy model with Poisson colonisation. $(0,0)$, the trivial steady state, corresponds to an empty landscape; $(p_s^*,0)$ is the semitrivial steady state where only sexuals dominate the landscape, while $(0,p_a^*)$ is the semitrivial steady state corresponding to dominance of asexuals; $(\hat{p}_s,\hat{p}_a)$ is the coexistence steady state. The other intersections of the zeroclines with the axes, p_s^g and p_a^f, are also indicated. Estimates of these intersection points help to determine conditions for stability of the different outcomes of the model.

To investigate if the zerocline $f_2(p_s, p_a) = 0$ intersects the p_s-axis in the region of interest ω, it suffices to notice that the following equation holds

$$f_2(p_s, 0) = \frac{(1 - \mathrm{e}^{-d_s p_s})(1 - \sigma)(1 - p_s)}{p_s} - \sigma = 0,$$

which determines a point $P_s^* := (p_s^*, 0)$ such that

$$\frac{(1 - \mathrm{e}^{-d_s p_s^*})(1 - p_s^*)}{p_s^*} = \frac{\sigma}{1 - \sigma}.$$

This point is in fact a steady state of the system, the one denoting fixation of sexuals. Knowing that $1 - \mathrm{e}^{-d_s p_s} \leq d_s p_s$ and that $\frac{1 - \mathrm{e}^{-d_s p_s}}{p_s} \geq 1 - \mathrm{e}^{-d_s}$ for $p_s \leq 1$ allow to find the following estimates for p_s^* :

$$1 - \frac{\sigma}{(1 - \sigma)(1 - \mathrm{e}^{-d_s})} \leq p_s^* \leq 1 - \frac{\sigma}{(1 - \sigma) d_s}. \tag{3.17}$$

Also, taking into account that $1 - \mathrm{e}^{-d_s p_s} \leq 1$, another upper bound for the value p_s^* is obtained so that

$$1 - \frac{\sigma}{(1 - \sigma)(1 - \mathrm{e}^{-d_s})} \leq p_s^* \leq 1 - \sigma. \tag{3.18}$$

It turns out that the equation $\frac{(1 - \mathrm{e}^{-d_s p_s^*})(1 - p_s^*)}{p_s^*} = \frac{\sigma}{1 - \sigma}$ has a unique solution $p_s^* \in [0, 1]$ if and only if $\frac{\sigma}{1 - \sigma} \in [0, d_s]$ (*i.e.* $0 \leq \mathcal{S} \leq 1$ is satisfied). Indeed, consider the function $k(p_s) = \frac{(1 - \mathrm{e}^{-d_s p_s})(1 - p_s)}{p_s}$ and notice that $k(0) = d_s$, $k(1) = 0$, and k is continuous. Therefore, there exists a solution p_s^*. To show uniqueness of the solution, notice that via implicit differentiation, the derivative of the function $p_a(p_s)$ obeys the following relations:

$$\frac{dp_a}{dp_s} = -\frac{\frac{\partial f_2(p_s, p_a)}{\partial p_s}\big|_{(p_s, p_a(p_s))}}{\frac{\partial f_2(p_s, p_a)}{\partial p_a}\big|_{(p_s, p_a(p_s))}} = -\frac{\frac{-\sigma}{p_s} + \frac{d_s \sigma}{\mathrm{e}^{d_s p_s} - 1} - \frac{\sigma}{1 - p_s - p_a(p_s)}}{-\sigma d_a - \frac{\sigma}{1 - p_s - p_a(p_s)}} < 0.$$

Thus, this zerocline is a strictly decreasing curve in the plane $p_s - p_a$. Hence it intersects the p_s-axis only once.

In a similar manner, it is possible to investigate the point where the curve $f_2(p_s, p_a) = 0$ intersects the p_a-axis. It is necessary, though, to consider the limiting value

$$\lim_{p_s \to 0} \frac{1}{p_s}(1 - \mathrm{e}^{-d_s p_s})(1 - \sigma)\mathrm{e}^{-d_a p_a}(1 - p_s - p_a) - \sigma,$$

as $f_2(0,0)$ is not defined for $p_s = 0$. In view of the fact that this limit is zero, due to the equation $f_2(p_s, p_a) = 0$, the following formula is obtained:

$$0 = d_s(1-\sigma)\mathrm{e}^{-d_a p_a}(1-p_a) - \sigma.$$

Thus, the intersection point of the zerocline with the axis $p_s = 0$ is a point $P_a^f := (0, p_a^f)$, where p_a^f is given implicitly by the equation

$$\mathrm{e}^{-d_a p_a^f}(1-p_a^f) = \frac{\sigma}{(1-\sigma)d_s}.$$

Notice that P_a^f denotes the intersection of the curve $f_2 = 0$ with the p_a-axis. It is not a steady state of the system under study.

Since there is not an explicit expression for p_a^f, it would be desirable to at least have some estimates of its value. To this end, consider now the function $h(p_a) = \mathrm{e}^{-d_a p_a}(1-p_a)$. It can be seen that $h(0) = 1$, $h(1) = 0$ and $h'(p_a) = -d_a \mathrm{e}^{-d_a p_a}(1-p_a) - \mathrm{e}^{-d_a p_a} < 0$, that is, h is a decreasing function. Notice also that $h(p_a^f) = \frac{\sigma}{(1-\sigma)d_s}$. From this information about h, more can be found out about the number p_a^f : if $\frac{\sigma}{(1-\sigma)d_s} > 1$, then $p_a^f < 0$; if $\frac{\sigma}{(1-\sigma)d_s} = 1$, then $p_a^f = 0$; if $\frac{\sigma}{(1-\sigma)d_s} < 1$, then $p_a^f > 0$; finally, if $\frac{\sigma}{(1-\sigma)d_s} = 0$, then $p_a^f = 1$. Moreover, due to the fact that $\mathrm{e}^{-d_a p_a} \leq 1$ when $p_a \geq 0$ and $\mathrm{e}^{-d_a p_a} \geq \mathrm{e}^{-d_a}$ for $p_a \leq 1$ it is possible to find the following estimates for the value of p_a^f

$$1 - \frac{\sigma}{(1-\sigma)d_s \mathrm{e}^{-d_a}} \leq p_a^f \leq 1 - \frac{\sigma}{(1-\sigma)d_s}. \tag{3.19}$$

This concludes the study of the behaviour of the zerocline $f_2(p_s, p_a) = 0$.

On the behaviour of the zerocline given by the equation $g_2(p_s, p_a) = 0$

The goal in this section is to study the curve $g_2(p_s, p_a) = 0$ in the $p_s - p_a$ plane. The arguments used will be absolutely similar to those in the previous section about the curve $f_2 = 0$. However, they will be given next for the sake of completeness. First, notice that the equation

$$g_2(p_s, p_a) = \frac{1}{p_a}(1 - \mathrm{e}^{-d_a p_a})(1-\alpha)(1-p_s-p_a) - \alpha = 0$$

implicitly defines a function $\tilde{p}_a(p_s)$ whose derivative is given by the following formula

$$\frac{d\tilde{p}_a}{dp_s} = -\frac{\frac{\partial g_2(p_s,p_a)}{\partial p_s}\big|_{(p_s,\tilde{p}_a(p_s))}}{\frac{\partial g_2(p_s,p_a)}{\partial p_a}\big|_{(p_s,\tilde{p}_a(p_s))}} = -\frac{-\frac{\alpha}{1-p_s-\tilde{p}_a(p_s)}}{-\frac{\alpha}{\tilde{p}_a(p_s)} + \frac{d_a\alpha}{e^{d_a\tilde{p}_a(p_s)-1}} - \frac{\alpha}{1-p_s-\tilde{p}_a(p_s)}} < 0.$$

Therefore, $\tilde{p}_a(p_s)$ is a strictly decreasing function of p_s.

This curve meets the p_a-axis at a point $P_a^* := (0, p_a^*)$ such that

$$\frac{1}{p_a^*}(1 - e^{-d_a p_a^*})(1 - p_a^*) = \frac{\alpha}{1-\alpha}.$$

This point is the steady state of the system where only asexuals are present. An estimate for the value of this point is given by

$$1 - \frac{\alpha}{(1-\alpha)(1-e^{-d_a})} \le p_a^* \le 1 - \frac{\alpha}{(1-\alpha)d_a}, \tag{3.20}$$

because it is known that $1 - e^{-d_a\tilde{p}_a} \le d_a\tilde{p}_a$ and $1 - e^{-d_a\tilde{p}_a} \ge 1 - e^{-d_a}$.

The point where the curve $g_2(p_s, p_a) = 0$ intersects the p_s-axis is given by a point $P_s^g := (p_s^g, 0)$, which is found by considering the limit

$$\lim_{\tilde{p}_a \to 0} \frac{1}{\tilde{p}_a}(1 - e^{-d_a\tilde{p}_a})(1-\alpha)(1 - p_s - \tilde{p}_a) - \alpha.$$

Knowing that this limit is zero, since $g_2(p_s, p_a) = 0$, a value p_s^g is found such that

$$1 - p_s^g = \frac{\alpha}{(1-\alpha)d_a},$$

which implies

$$p_s^g = 1 - \frac{\alpha}{(1-\alpha)d_a}, \tag{3.21}$$

this being the only intersection point that can be fully identified.

This is the point where it has been made evident that explicit expressions for the steady states of the system (3.6)–(3.7) cannot be given. The analysis of the model has to rely on the estimates found above. Also, it will be impossible to apply the techniques for the analysis of a system of two nonlinear difference equations, as was done before for the system with uniform colonisation probabilities (3.8), because the corresponding Jacobian matrix cannot be evaluated at the steady states. Therefore, it will be necessary to use a reasoning similar to that used in case (iv) of the simplified-colonisation version. That is, noticing that the matrix $J(p_s^0, p_a^0) - I$ is a translation to the origin of the system under study, it will be possible to find out if the corresponding eigenvalues are less than 1. However, it is not possible to say if their moduli are also less than 1, which is the criterion to investigate the stability of a steady state of a system of nonlinear difference equations. Thus, the discussion that follows may lead to conditions for existence and stability that are more relaxed than the system requires. However, numerical simulations backing these observations up, presented later in this chapter, suggest that the conditions found are a good approximation to the real behaviour of the system.

On the trivial and semi-trivial steady states

In the previous section, estimates for the points where the zeroclines $f_2 = 0$ and $g_2 = 0$ meet the coordinate axes in the $p_s - p_a$ plane were found. Some of these points were also steady states of the system. For them, the estimates found were

$$1 - \frac{\sigma}{(1-\sigma)(1-\mathrm{e}^{-d_s})} \leq p_s^* \leq 1 - \frac{\sigma}{(1-\sigma)d_s}$$

and

$$1 - \frac{\alpha}{(1-\alpha)(1-\mathrm{e}^{-d_a})} \leq p_a^* \leq 1 - \frac{\alpha}{(1-\alpha)d_a},$$

where the presence of the numbers $\mathcal{S} = \frac{\sigma}{(1-\sigma)d_s}$ and $\mathcal{A} = \frac{\alpha}{(1-\alpha)d_a}$ is once again noticed. These numbers influence the behaviour of the system in the following way:

Empty landscape. When $\mathcal{S} > 1$ and $\mathcal{A} > 1$, the only steady state of the system in the region of biological interest ω is the trivial equilibrium point $(0,0)$. At this point, both eigenvalues of the corresponding matrix $J(0,0) - I$ are both negative, which shows that $(0,0)$ is stable. The situation depicted here is BRR < 1 for both sexuals and asexuals. That is, their respective mortality rates are greater than their respective colonisation rates and eventually both morphs disappear from the landscape.

Fixation of sexuals. If $\mathcal{S} < 1$ and $\mathcal{A} > 1$, the previous steady state becomes unstable, as one of the eigenvalues becomes positive, and a new stable steady state emerges, $(p_s^*, 0)$, which corresponds to a landscape where only sexuals are present. In this case, $\sigma < (1-\sigma)d_s$. The mortality rate of sexuals is less than their colonisation rate while the corresponding BRR for asexuals is still less than 1.

Fixation of asexuals. The reverse situation is given by $\mathcal{S} > 1$ and $\mathcal{A} < 1$. Only asexuals are present in the landscape because their BRR is greater than 1, while that of sexuals makes their mortality rate greater than their colonisation rate. Of the two equilibrium points in ω, $(0, p_a^*)$ is stable and $(0,0)$ is unstable.

About the coexistence point

As said before, the coexistence steady state will be given by the intersection of the zeroclines $f_2(p_s, p_a) = 0$ and $g_2(p_s, p_a) = 0$. When they meet in the way depicted in figure 3.3, the kind of intersection between the zeroclines that may possibly give stability is obtained. Otherwise, there will be an unstable coexistence point. In both cases, the inequalities $\mathcal{S} < 1$ and $\mathcal{A} < 1$ hold, which makes both morphs present in the landscape because their mortality rates do not exceed their colonisation rates.

Stable coexistence is only attained when the following conditions are met:

$$p_s^* < p_s^g \quad \text{and} \quad p_a^f > p_a^*. \tag{3.22}$$

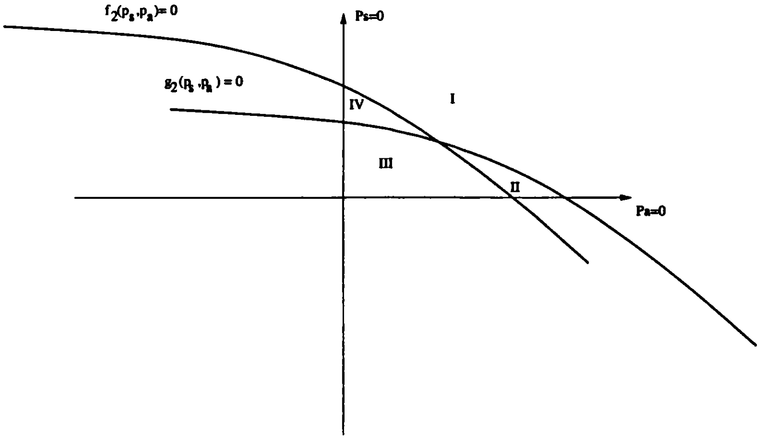

Figure 3.3: The intersection of zeroclines $f_2(p_s, p_a) = 0$ and $g_2(p_s, p_a) = 0$ is in the first quadrant of (p_s, p_a) plane, now divided into regions I, II, III and IV.

Indeed, in this case the eigenvalues of the matrix $J(\hat{p}_s, \hat{p}_a) - I$ are both negative, which implies that the eigenvalues of the matrix $J(\hat{p}_s, \hat{p}_a)$ are both less than 1, opening the possibility for stable coexistence. Therefore, it is necessary to understand when the conditions in (3.22) are met. Notice that the inequalities (3.19)–(3.21) justified above can be used to provide sufficient conditions for (3.22) to hold. Indeed, if one chooses parameters α, σ, d_s and d_a in such a way that

$$1 - \sigma < 1 - \frac{\alpha}{(1-\alpha)d_a} \tag{3.23}$$

and

$$1 - \frac{\alpha}{(1-\alpha)d_a} < 1 - \frac{\sigma}{(1-\sigma)d_s \mathrm{e}^{-d_a}}, \tag{3.24}$$

then, on the one hand, due to (3.18) and (3.21),

$$p_s^* \leq 1 - \sigma < 1 - \frac{\alpha}{(1-\alpha)d_a} = p_s^g;$$

on the other hand, in view of (3.19) and (3.20),

$$p_a^f \leq 1 - \frac{\alpha}{(1-\alpha)d_a} < 1 - \frac{\sigma}{(1-\sigma)d_s \mathrm{e}^{-d_a}} \leq p_a^*.$$

One would like to know next whether it is possible to ensure that the inequalities (3.23) and (3.24) both hold. Since it is required that

$$1 - \sigma < 1 - \frac{\alpha}{(1-\alpha)d_a} < 1 - \frac{\sigma}{(1-\sigma)d_s \mathrm{e}^{-d_a}},$$

those suitable values of α constitute the interval

$$\frac{\frac{d_a \sigma \mathrm{e}^{d_a}}{(1-\sigma)d_s}}{1 + \frac{d_a \sigma \mathrm{e}^{d_a}}{(1-\sigma)d_s}} < \alpha < \frac{\sigma d_a}{1 + \sigma d_a}. \tag{3.25}$$

It should be remarked that the inequalities (3.25) are obtained under the assumption that the right-hand inequality in (3.18) provides a better estimate for p_s^* than the right-hand inequality in (3.17), which happens if $(1-\sigma)d_s \geq 1$ is satisfied. Otherwise, that is, if $(1-\sigma)d_s < 1$, one should use (3.17) rather than (3.18) in the argument above. Notice also that if

$$(1-\sigma)d_s > \mathrm{e}^{d_a}, \tag{3.26}$$

which automatically fulfils the inequality $(1-\sigma)d_s > 1$, then $1 - \sigma < 1 - \frac{\sigma}{(1-\sigma)d_s \mathrm{e}^{-d_a}}$ and, consequently, the interval (3.25) is not empty.

It is crucial to recall that all the preceding arguments rely on estimates for the numbers p_s^*, p_a^f, and p_a^*, rather than on any explicit expressions for them because, unlike p_s^g, none of these numbers can be directly obtained from the consideration of the zeroclines of the original Poisson-colonisation system, the related equations being transcendental. Even though it was said before that the fact that one cannot investigate in full the moduli of the eigenvalues may give a picture more optimistic than reality, it is also possible that all conditions set by the estimates in this part of the analysis could be relaxed, allowing for wider ranges where stable coexistence would occur. The analysis, however, has been restricted to intervals where it is absolutely certain that a stable polymorphism will be found. An example shall be provided next.

An illustration of coexistence where $\sigma > \alpha$

Let us choose values for parameters d_s, d_a, σ and α that comply with the conditions (3.25) given in the previous section. For this, it is convenient to choose first values of σ, d_s and d_a satisfying (3.26), and then pick a value α somewhere in the interval specified by the inequalities (3.25). Thus, let $d_s = 6$, $d_a = 1$, $\sigma = 0.5$ and $\alpha \in (0.311, 0.333)$, say $\alpha = 0.320$. Then, the phase diagram in figure 3.4 is obtained.

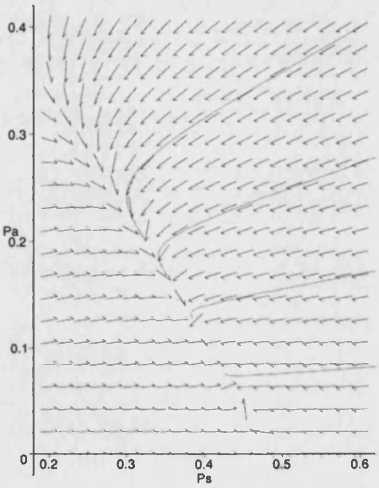

Figure 3.4: The figure shows a numerical simulation of the phase diagram of the dynamical system. The parameter regime is such that stable coexistence is observed. The values of the parameters are: $d_s = 6$, $d_a = 1$, $\sigma = 0.5$ and $\alpha = 0.32$.

These figures do give evidence for stability. Moreover, direct numerical simulations of the equations (3.6) and (3.7) confirm that this is a stable coexistence point. The interval in which the values of α lie in this example of stable coexistence suggests that this is not the only point where this outcome can be witnessed, and numerical simulations have also confirmed the existence of a non-negligible region of stable coexistence points in the $p_s - p_a$ plane. This is later investigated with full detail in a study of the parameter space.

A different instance of stable coexistence: $\sigma < \alpha$

In the previous sections, conditions and values for the parameters of the model were found so that it exhibits stable coexistence. This was done by fixing d_s, d_a, and σ and thus finding an interval for values of α. The values obtained, however, were such that $\sigma > \alpha$. This makes sexuals more vulnerable to environmental challenges than asexuals[1]. An example where sexuals are competitively dominant will be given now. That is, a choice of parameter values where $\sigma < \alpha$, $d_s > d_a$ and the system still exhibits stable coexistence.

Again, to fulfil the conditions in (3.22), it is necessary to find values for the parameters such that (*cf.* (3.25))

$$\frac{\frac{d_a \sigma \mathrm{e}^{d_a}}{(1-\sigma)d_s}}{1+\frac{d_a \sigma \mathrm{e}^{d_a}}{(1-\sigma)d_s}} < \alpha < \frac{\sigma d_a}{1+\sigma d_a}. \tag{3.27}$$

If one imposes the condition

$$d_a \mathrm{e}^{d_a} < d_s \tag{3.28}$$

on the parameters d_s and d_a, then (*cf.* the left-hand side inequality in (3.27))

$$\frac{\frac{d_a \sigma \mathrm{e}^{d_a}}{(1-\sigma)d_s}}{1+\frac{d_a \sigma \mathrm{e}^{d_a}}{(1-\sigma)d_s}} < \sigma.$$

Thus, if the inequality (3.28) is satisfied, then making sure that

$$\sigma < \alpha < \frac{\sigma d_a}{1+\sigma d_a} \tag{3.29}$$

will provide the required values for α. Hence, choosing first a value for σ, then for d_a in such a way that $\sigma < \frac{\sigma d_a}{1+\sigma d_a}$, and finally, for α according to (3.29), and for d_s so that (3.28) holds, the task set in the previous paragraph is achieved. Note that, importantly, the inequality (3.28) implies that sexuals are better dispersers, that is $d_s > d_a$.

Using the procedure outlined above, let $\sigma = \frac{3}{16}$ and then $d_a = 2$, $\alpha = \frac{1}{4}$ and $d_s = 20$. Figure 3.5 shows the curves $f_2 = 0$ and $g_2 = 0$ for this choice of parameter values.

The corresponding phase diagram is given in figure 3.6.

Once again, these results are backed up by numerical experiments. More general observations are possible when different parameter spaces are considered.

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[1] The case when $\sigma < \alpha$ is not biologically contradictory when environmental factors contributing to mortality are biotic (*e.g.* pathogens). In habitats where these biotic factors are unimportant, α could be less than σ if abiotic factors (*i.e.* physical) contribute to mortality (*e.g.* cold winters). The most famous explanation for this is that asexuals have been selected for the acquisition of general-purpose genotypes that enable them to survive under a wide range of environmental conditions. This has been most forcefully argued by Lynch (1984).

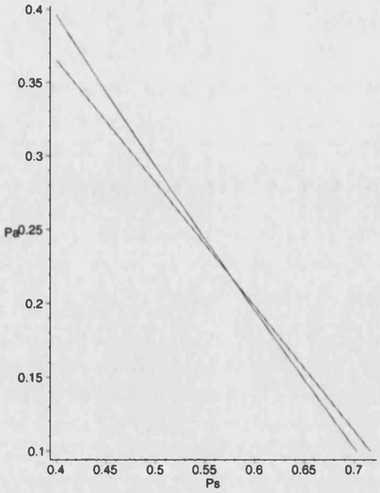


Figure 3.5: The intersection of the nontrivial zeroclines $f_2 = 0$ and $g_2 = 0$. The values of the parameters for this simulation are $\sigma = \frac{3}{16}$, $d_a = 2$, $\alpha = \frac{1}{4}$ and $d_s = 20$.

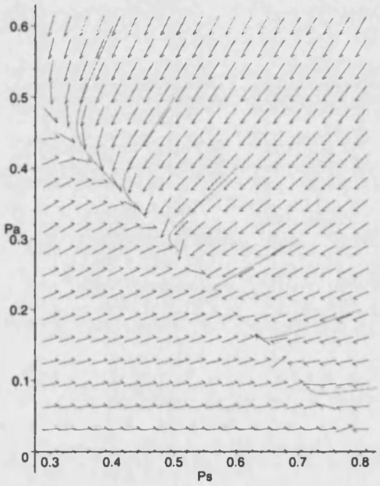


Figure 3.6: Phase diagram of a numerical simulation where $\sigma = \frac{3}{16}$, $d_a = 2$, $\alpha = \frac{1}{4}$ and $d_s = 20$. Stable coexistence is observed. In this example, sexuals are the stronger type since $d_s > d_a$ and $\sigma < \alpha$.

This will be done next.

3.1.5 Study of the parameter space

Reading through the last two examples leaves the impression that finding the numbers that will produce the desired result and graph is a matter of luck. It may be indeed so when one is getting familiar with the equations and trying the first few simulations, but later it becomes evident that a detailed study of the parameter space may allow the characterisation of regions where the different outcomes of the model take place.

The parameter space is, in principle, four-dimensional. This is impossible to visualise and very difficult to study. Therefore, it will be restricted to two-dimensional subspaces obtained when d_s and d_a are fixed and the mortality rates vary over $[0, 1]$, or when σ and α are fixed and the dispersal coefficients vary from zero to infinity. Let d_s^0 and d_a^0 be the fixed values for the dispersal coefficients. Then, on the $\sigma - \alpha$ plane two straight lines that divide the $[0, 1] \times [0, 1]$ region in four subregions can be distinguished, as shown in figure 3.7. The straight lines are $\sigma = \frac{d_s^0}{1+d_s^0}$ and $\alpha = \frac{d_a^0}{1+d_a^0}$. In region I, where $\sigma > \frac{d_s^0}{1+d_s^0}$ and $\alpha > \frac{d_a^0}{1+d_a^0}$, it is known that $(0, 0)$ is the only steady state in ω and that it is stable. This means that for any set of parameters $(d_s^0, d_a^0, \sigma, \alpha)$ in this region, the outcome of the model will be an empty landscape. In region II, where $\sigma > \frac{d_s^0}{1+d_s^0}$ and $\alpha < \frac{d_a^0}{1+d_a^0}$, it is known that $(0, p_a^*)$, the purely asexual steady state is stable while $(0, 0)$ has become unstable and fixation of asexuals is expected for any choice of parameters in this region. Analogously, when $\sigma < \frac{d_s^0}{1+d_s^0}$ and $\alpha > \frac{d_a^0}{1+d_a^0}$, in region IV, the outcome of the model will be the fixation of sexuals.

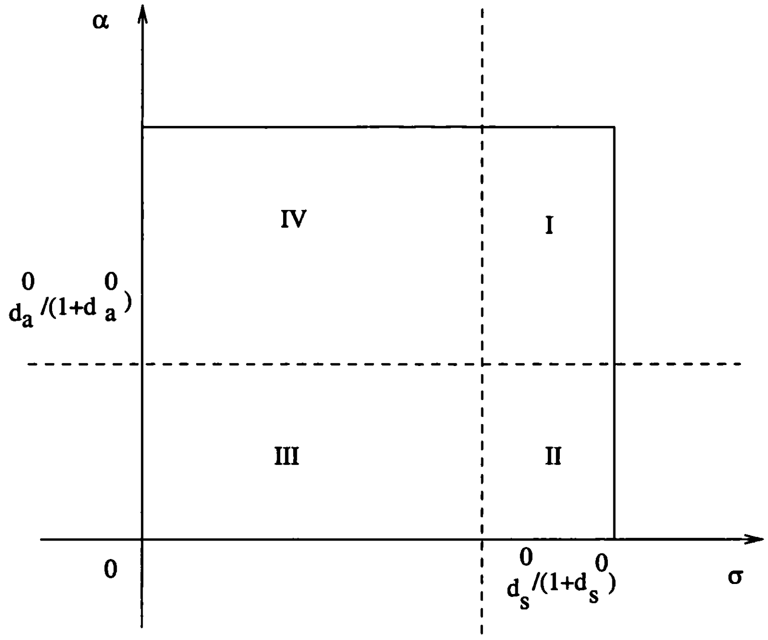


Figure 3.7: For fixed dispersal coefficients, the parameter space $\sigma - \alpha$ is divided in four regions as shown in this figure. Region I corresponds to parameter regimes where $(0, 0)$ is the only steady state and it is stable. Parameter values chosen in region II will lead to fixation of asexuals, while those in region IV lead to fixation of asexuals. When parameters are chosen in region III, both fixation of either type or stable coexistence is possible. This region is shown in detail in a later figure.

Only region III is left to examine. Here, both $\mathcal{S} < 1$ and $\mathcal{A} < 1$. There is scope for different results, among which there is coexistence, but also fixation of sexuals or asexuals. The task now is to try to find the boundaries, within region III, that separate these outcomes. In figure 3.8, it can be seen that the different possibilities are described by the following inequalities: (i) $p_s^* > p_s^g$ and $p_a^f > p_a^*$, (ii) $p_s^* < p_s^g$ and $p_a^f > p_a^*$, (iii) $p_s^* < p_s^g$ and $p_a^f < p_a^*$ and (iv) $p_s^* > p_s^g$ and $p_a^f < p_a^*$. It is the transition between these cases, moving continuously over region IV, given by the equalities $p_s^* = p_s^g$ and $p_a^f = p_a^*$, that implicitly define the boundaries looked for, given by the curves:

$$\mathcal{S} = \frac{1 - \mathrm{e}^{-d_s(1-\mathcal{A})}}{d_s(1-\mathcal{A})}\mathcal{A}$$

and

$$\mathrm{e}^{\frac{-d_a(1-\mathcal{S})}{\mathcal{A}d_a+1}} \frac{\mathcal{A}d_a + \mathcal{S}}{\mathcal{A}d_a + 1} = \mathcal{S}.$$

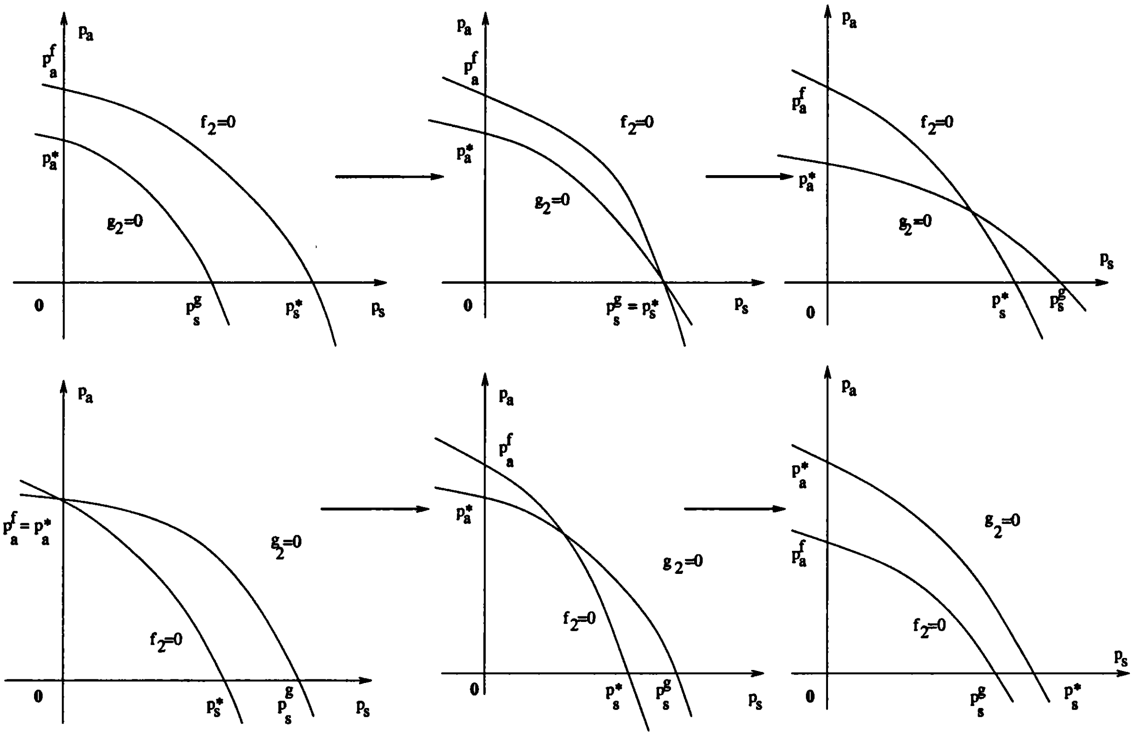


Figure 3.8: Different possible outcomes in region III are determined by the way the nontrivial zeroclines intersect. The figure shows how obtaining one semi-trivial steady state or a coexistence result depends on this intersection.

In a similar way, σ^0 and α^0 can be fixed values for the mortality rates and the resulting $d_s - d_a$ plane, divided in four regions by the two straight lines $d_s = \frac{\sigma^0}{1-\sigma^0}$ and $d_a = \frac{\alpha^0}{1-\alpha^0}$, as shown in figure 3.9, can be studied. Region I is now the region where all different kinds of outcomes may be expected, while a choice of parameters in region II will give fixation of sexuals. A set of parameters chosen within region III will lead to fixation of asexuals and in region IV an empty landscape is the only stable outcome. Boundaries for the different outcomes within region I are found following a strategy analogous to the one described above.

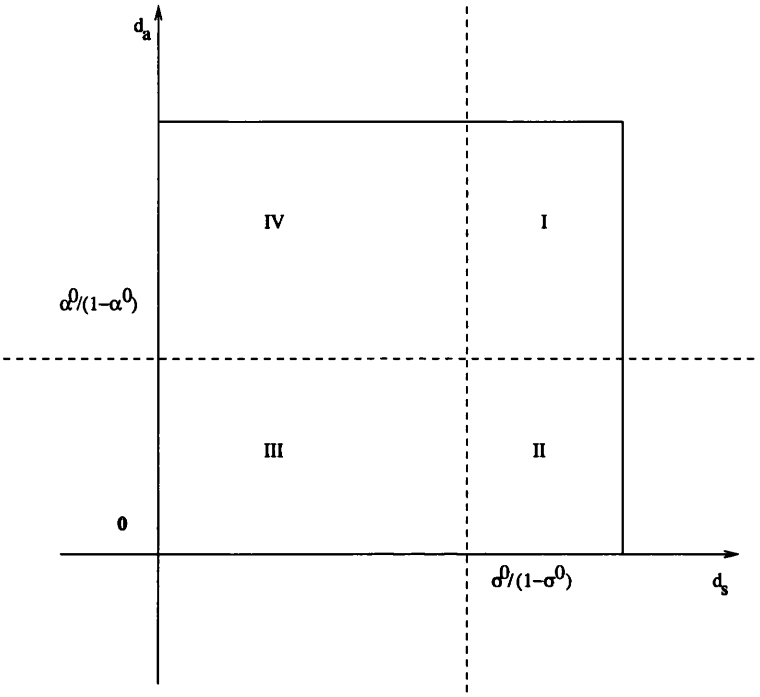


Figure 3.9: The parameter space $d_s - d_a$ is divided in four regions for fixed mortality rates. Region III corresponds to parameter settings where an empty landscape is the only possible, and stable, outcome of the model. Fixation of sexual and asexual is seen for parameter settings in regions II and IV, respectively. Finally, region I corresponds to parameter values where both fixation and coexistence are possible. This region is looked at in a later figure.

Figures 3.10 and 3.11 show illustrations of the previous ideas. There, the two-dimensional $\sigma - \alpha$ plane for fixed d_s and d_a and the two-dimensional $d_s - d_a$ plane for fixed σ and α are depicted, respectively. Different symbols represent the different possible outcomes of the model: (o), fixation of sexuals; (x), fixation of asexuals; ( ), empty landscape; (+), unstable coexistence and (*), stable coexistence of both types. The regions where they could in principle be found are also shown, taking into account that all previous observations are valid as far as only part of the stability criteria, that when the eigenvalues are less than 1, is concerned.

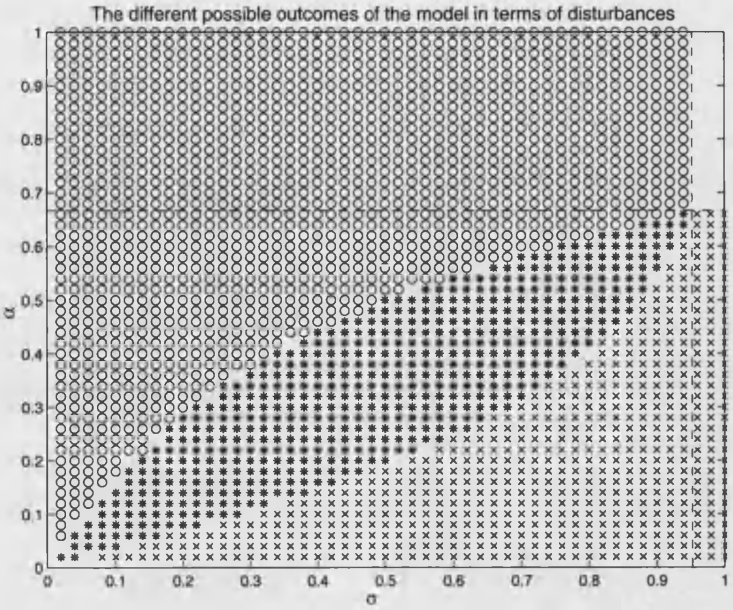


Figure 3.10: The figure shows an example of the results of the model distributed on a $\sigma - \alpha$ parameter space for fixed dispersal coefficients $d_s^0 = 20$ and $d_a^0 = 2$. The code of symbols is: (o), fixation of sexuals; (x), fixation of asexuals; ( ), empty landscape; and (*), stable coexistence of both types.

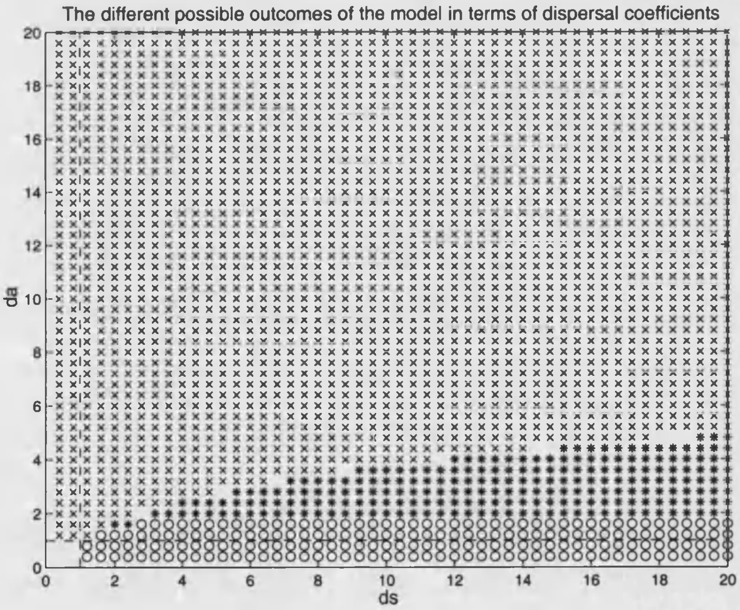


Figure 3.11: For fixed mortality rates $\sigma^0 = 0.5$ and $\alpha^0 = 0.5$, the $d_s - d_a$ parameter space in the figure is obtained. Possible results are shown by the code of symbols: (o), fixation of sexuals; (x), fixation of asexuals; ( ), empty landscape; and (*), stable coexistence of both types.

3.2 Inclusion of male function in asexuals

In the previous metapopulation model, one key aspect of the biological situation that motivates the model was left out: male function in asexuals. Sexuals and

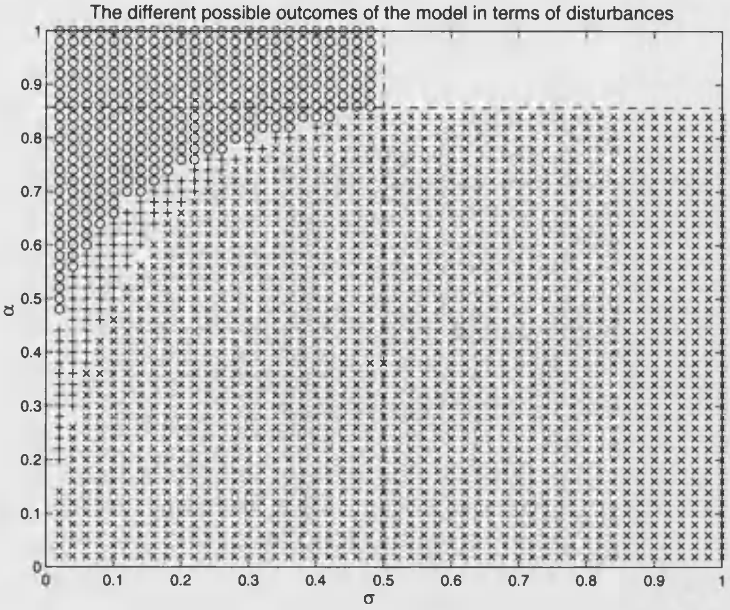


Figure 3.12: In this example of a $\sigma - \alpha$ parameter space for fixed dispersal coefficients $d_s^0 = 6$ and $d_a^0 = 1$, the parameters are such that only unstable coexistence is seen in region III. A symbol (+) shows the distribution of this result in the parameter space.

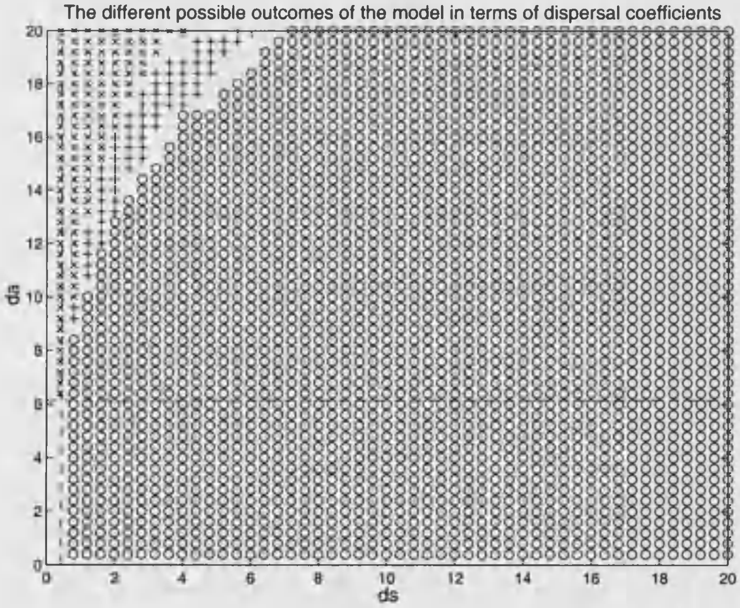


Figure 3.13: For fixed mortality rates $\sigma^0 = 0.1$ and $\alpha^0 = 0.8$, the $d_s - d_a$ parameter space is as shown in the figure. Only unstable coexistence is obtained in this example too, signalled by (+).

asexuals join their paths through this aspect of the problem. Both sexual and asexual offspring are generated when the male gametes produced by the male function of asexuals fertilise the eggs produced by sexual females. When male function is included, the colonisation of empty patches will not be proportional to the number of patches occupied by each morph as before, when propagules arrived in empty patches at rates $d_s p_s$ and $d_a p_a$, but will rather depend on the proportions of the different types of offspring that are generated through sexual-sexual or sexual-asexual crosses and parthenogenesis. The new rates of arrival will thus be given by $d_s \bar{p}_s$ and $d_a \bar{p}_a$, where $\bar{p}_s$ represents the proportion of sexual offspring and $\bar{p}_a$ the proportion of asexual offspring generated in one reproductive episode of the population. From the model of temporal dynamics in chapter 2, it is easy to see that such proportions are given by the following expressions

$$\bar{p}_s := \frac{\mu p_s \frac{p_s + g_s p_a}{p_s + (1-u) p_a}}{\mu p_s + p_a}, \tag{3.30}$$

and

$$\bar{p}_a := \frac{\mu p_s \frac{g_a p_a}{p_s + (1-u) p_a} + p_a}{\mu p_s + p_a}. \tag{3.31}$$

Thus, the following system of equations is obtained

$$p_s(t+1) = \bar{C}_s(1-\sigma)(1-\bar{C}_a)(1-p_s(t)-p_a(t)) + (1-\sigma)p_s(t) \tag{3.32}$$

and

$$p_a(t+1) = \bar{C}_a(1-\alpha)(1-p_s(t)-p_a(t)) + (1-\alpha)p_a(t) \tag{3.33}$$

to represent a patch-occupancy model where male function is included. Notation parallel to that in the simpler patch-occupancy model in (3.32) and (3.33) is used, but it must be noted that the colonisation probabilities are now given by $\bar{C}_s := 1 - \mathrm{e}^{-(d_s \bar{p}_s + d_a \bar{p}_a)}$ and $\bar{C}_a := 1 - \mathrm{e}^{-(d_s \bar{p}_s + d_a \bar{p}_a)}$. (*N.B.* For brevity, the argument t has been omitted in $\bar{p}_s$ and $\bar{p}_a$, in p_s and p_a in formulas (3.30) and (3.31), as well as in $\bar{C}_s$ and $\bar{C}_a$. For the same reason, the bar on the colonisation probabilities are henceforth dropped.)

As before, the interest is in finding the conditions under which system (3.32)–(3.33) reaches equilibrium. Consider the expression

$$\Delta p_s =: F(p_s(t), p_a(t)) = f_1(p_s(t), p_a(t)) f_2(p_s(t), p_a(t)),$$

where

$$f_1(p_s, p_a) := p_s$$

and

$$f_2(p_s, p_a) := \frac{1}{p_s} C_s(1-\sigma)(1-C_a)(1-p_s-p_a) - \sigma.$$

It describes changes in the fraction of patches occupied by sexuals. As far as notation is concerned, one could be more strict and use, say, $\bar{F}$, $\bar{f}_1$ and $\bar{f}_2$, but this would only make writing and reading cumbersome. Therefore, the reader is asked to notice that although the notation for these functions has been kept the same as before, the functions are different from those in the model without male function in asexuals. Similarly, for changes in the value of p_a, consider

$$\Delta p_a =: G(p_s(t), p_a(t)) = g_1(p_s(t), p_a(t)) g_2(p_s(t), p_a(t)),$$

where

$$g_1(p_s, p_a) := p_a$$

and

$$g_2(p_s, p_a) := \frac{1}{p_a} C_a(1-\alpha)(1-p_s-p_a) - \alpha.$$

The zeroclines of the system (3.32)–(3.33) are given by the equations $f_1(p_s, p_a) = 0$, $f_2(p_s, p_a) = 0$, $g_1(p_s, p_a) = 0$ and $g_2(p_s, p_a) = 0$. Some of the intersections of these curves are the steady states of the system. These intersections of interest are (i) $(0, 0)$, intersection of the lines $p_s = 0$ and $p_a = 0$; (ii) $(p_s^*, 0)$, the intersection of the curve $f_2(p_s, p_a) = 0$ and the axis $p_a = 0$; (iii) $(0, p_a^*)$, the intersection of the curve $g_2(p_s, p_a) = 0$ and the axis $p_s = 0$; finally, (iv) $(\hat{p}_s, \hat{p}_a)$, the polymorphic steady state that may be stable or unstable, according to the way in which the zeroclines $f_2(p_s, p_a) = 0$ and $g_2(p_s, p_a) = 0$ intersect.

As a result, in order for the polymorphic steady state to be stable, the following conditions must be satisfied:

$$\frac{(1-\sigma)(1-\mathrm{e}^{-d_s})}{(1-\sigma)(1-\mathrm{e}^{-d_s}) + \sigma} < \frac{(1-\alpha)d_a(\mu g_a + 1)}{(1-\alpha)d_a(\mu g_a + 1) + \alpha\mu}, \tag{3.34}$$

and

$$\frac{(1-\alpha)(1-\mathrm{e}^{-d_a})}{(1-\alpha)(1-\mathrm{e}^{-d_a}) + \alpha} < \frac{(1-\sigma)d_s\mu g_s \mathrm{e}^{-d_a}}{(1-\sigma)d_s\mu g_s \mathrm{e}^{-d_a} + \sigma(1-u)}, \tag{3.35}$$

while for it to be unstable, the corresponding conditions are

$$\frac{(1-\sigma)(1-\mathrm{e}^{-d_s})}{(1-\sigma)(1-\mathrm{e}^{-d_s}) + \sigma} > \frac{(1-\alpha)d_a(\mu g_a + 1)}{(1-\alpha)d_a(\mu g_a + 1) + \alpha\mu}, \tag{3.36}$$

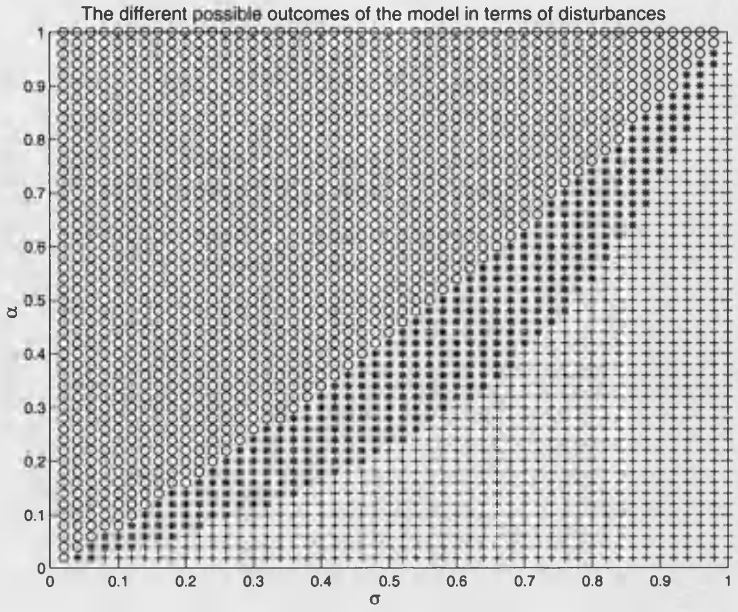


Figure 3.14: The figure shows the parameter space for fixed dispersal coefficients $d_s = 6$ and $d_a = 1$, in the modified model which includes male function in asexuals. This more biologically realistic model exhibits the same behaviour of its simpler counterpart, only with modified regions of distribution for the different outcomes (*cf.* figure 3.10). The code of symbols is the same: stable coexistence (*), invasion of sexuals (o) and invasion of asexuals (+). Other parameters are set as follows: $\mu = 1$, $g_s = g_a = 0.25$, and $u = 0.5$.

and

$$\frac{(1-\alpha)(1-\mathrm{e}^{-d_a})}{(1-\alpha)(1-\mathrm{e}^{-d_a})+\alpha} > \frac{(1-\sigma)d_s\mu g_s\mathrm{e}^{-d_a}}{(1-\sigma)d_s\mu g_s\mathrm{e}^{-d_a}+\sigma(1-u)}. \tag{3.37}$$

An analysis of the parameter space with fixed dispersal coefficients and variable mortality rates, allows the establishment of conditions for the existence of the different outcomes of the model. Both regions of stable and unstable coexistence are possible, depending on the relation between two key numbers $c_1 = \frac{\mu(1-\mathrm{e}^{-d_s})}{d_a(\mu g_a+1)}$ and $c_2 = \frac{d_s\mu g_s}{(1-u)(\mathrm{e}^{-d_a}-1)}$. Thus, the following result is obtained:

Proposition. Stable coexistence is possible if and only if $c_1 < c_2$. In this case, the region of stable coexistence is bounded by two hyperbolas in the σ–α plane given by the equations $\sigma = \frac{c_1\alpha}{1+(c_1-1)\alpha}$ and $\sigma = \frac{c_2\alpha}{1+(c_2-1)\alpha}$. Consequently, unstable coexistence is possible if and only if $c_1 > c_2$.

Instead of a proof, which derives painstakingly from the study of conditions (3.34)–(3.37) and would only make the reader tired or confused, numerical simulations for cases where the model including male function exhibits stable (figure 3.14) and unstable (figure 3.15) coexistence are given.

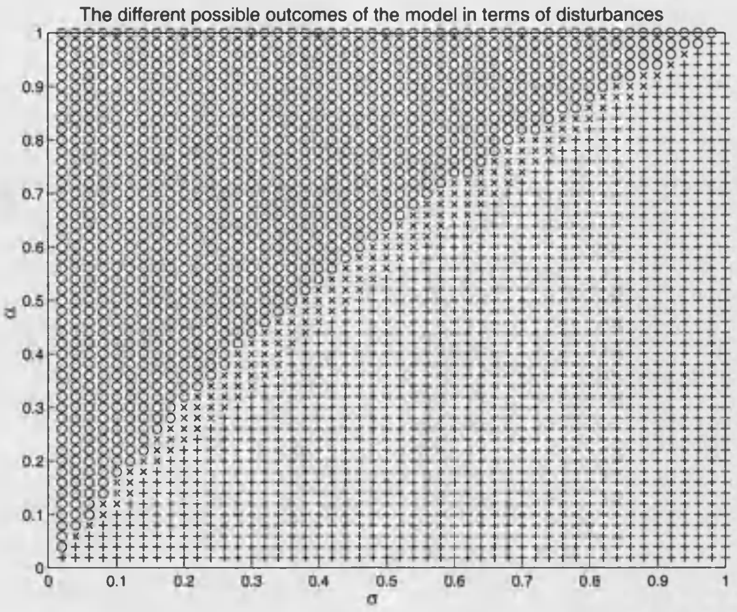


Figure 3.15: In this example of fixed dispersal coefficients, $d_s = 1$ and $d_a = 1$, unstable coexistence (x), invasion of sexuals (o) and invasion of asexuals (+) are the outcomes of the model modified to include male function in asexuals. Other parameters are: $\mu = 1$, $g_s = g_a = 0.25$, and $u = 0.5$.

3.3 Discussion

The models in this chapter work with four fundamental parameters: mortality rate for sexuals, σ, and asexuals, α, as well as dispersal coefficient for sexuals, d_s, and asexuals, d_a. It is in terms of these parameters that two key numbers in the analysis, $\mathcal{S} = \frac{\sigma}{d_s(1-\sigma)}$ and $\mathcal{A} = \frac{\alpha}{d_a(1-\alpha)}$, have been defined. The values of these numbers dictate the number of steady states in Ω, the region of biological interest, and the behaviour of the three models, as seen in their analyses. That is, exact conditions are given for: (i) the disappearance of both morphs from the landscape; (ii) the prevalence of sexuals and the disappearance of asexuals; (iii) the reverse situation where only asexuals remain in the landscape while sexuals disappear; (iv) the coexistence of both morphs and the stability or instability of the these outcomes. Furthermore, the inverse of $\mathcal{S}$ and $\mathcal{A}$ are the basic reproductive rates of sexuals,

$$R_s := \frac{d_s(1-\sigma)}{\sigma} = \frac{1}{\mathcal{S}},$$

and of asexuals,

$$R_a := \frac{d_a(1-\alpha)}{\alpha} = \frac{1}{\mathcal{A}},$$

where

$$\text{Basic Reproductive Rate} = \frac{\text{colonisation rate}}{\text{mortality rate}}.$$

The BBR gives information about the number of patches a sexual or asexual individual is able to colonise before its death. The prevalence of a particular morph in the landscape was characterised in mathematical terms as BRR > 1, which means that colonisation rate should be greater than mortality rate for a morph not to disappear from the population. Based on the numbers introduced above, it was also possible to understand why the patch-occupancy model is capable of exhibiting stable coexistence, which is the result that had eluded previous modelling attempts of the dynamics of mixed populations. To fully develop this part of the discussion, information borrowed from the uniform-colonisation version of the model is very useful.

The model with uniform colonisation gives exact conditions for all the previous outcomes, also in terms of $\mathcal{S}$ and $\mathcal{A}$. The two models coincide in their prediction that if the mortality rate of a morph exceeds its colonisation rate, then it will disappear from the landscape. However, in the uniform-colonisation model stable coexistence is not possible. At $(0,0)$, the sexual basic reproductive rate is R_s. When the system with Poisson colonisation reaches the purely sexual steady state $(p_s^*, 0)$, this rate is 1. It has been reduced by a factor $\frac{1}{R_s}$. When the distribution of propagules is uniform, that is, when the number of patches colonised per patch occupied, $\frac{dp}{p} = d$, does not depend on the number of occupied patches, the effect on the asexual basic reproductive rate will be the same and it will be reduced as $\frac{R_a}{R_s}$. As was seen in the analysis, $\mathcal{A} < \mathcal{S}$ or $R_a > R_s$ or $\frac{R_a}{R_s} > 1$ is a necessary and sufficient condition to make $(p_s^*, 0)$ susceptible to invasion by asexuals, since asexuals are better colonisers. As for asexuals, at $(0,0)$ their basic reproductive rate is R_a. As the system with Poisson colonisation reaches the purely asexual steady state $(0, p_a^*)$, this rate becomes 1, thus reduced by a factor $\frac{1}{R_a}$. The effect on sexuals is the same plus a factor to account for their weaker competition at colonisation. Therefore, $\frac{R_s}{R_a} > 1$ doesn't guarantee invasion of $(0, p_a^*)$ by sexuals. Now, $\frac{R_a}{R_s} > 1$ and $\frac{R_s}{R_a} > 1$ cannot both hold. Stable coexistence is therefore impossible via the linear approximation to the original Poisson colonisation process. With a Poisson distribution of propagules, $\frac{R_a}{R_s} > 1$ or $\frac{R_s}{R_a} > 1$ are no longer necessary conditions for invasion. Moreover, in this model, the number of patches colonised per patch occupied is now given by $f(p) = \frac{1-e^{-dp}}{p}$, which is a decreasing function of p. That is, rare types are favoured, making $(p_s^*, 0)$ and $(0, p_a^*)$ susceptible to invasion by the rarely represented morph and stable coexistence plausible. It can now be seen how the information lost to the linear approximation to the Poisson process makes it impossible to obtain stable coexistence. However, the results in the uniform-colonisation case shed light on the interpretation of the results obtained from the analysis of the Poisson model, where stable coexistence is possible.

The model incorporates a patchy and unpredictable environment that is changing from one generation to the next. Some authors believe that the variable offspring produced by sexuals may, by chance, incorporate genotypes suited to the new patches. These authors also consider asexuals incapable of such variation (Greenwood and Adams, 1987). This is known as Williams' raffle analogy, or lottery models (1975). Although Williams' arguments have been outlived (see chapter 1), the lottery hypothesis can still be analysed, by means of the models in this chapter, to obtain an idea of the trade-off that goes on between a species holding on to occupied territory and it colonising new territory. Let us consider, first, the purely sexual steady state of Case II. It is being assumed then that only sexuals have survived the calamities of the environment. The fraction of patches occupied by this morph is given by $1 - \mathcal{S}$. Notice that, as is to be expected, this number is a decreasing function of σ, the probability that a perturbation affects colonisation or persistence, while it is an increasing function of d_s, the dispersal coefficient of sexuals. The same is true for $1 - \mathcal{A}$, the fraction of patches occupied by asexuals when they reach fixation, with respect to α and d_a respectively. Which parameter has a greater influence on the fraction of patches that remains occupied by sexuals/asexuals when the system reaches a fixed monomorphic point? That is, is the dispersal coefficient of the species ever enough to override the adverse effects of environmental perturbations? To answer this question, one needs to investigate the behaviour of $1-\mathcal{S}$ as a function of both σ and d_s. In order to do this, $\left|\frac{\partial S}{\partial d_s}\right|$ *vs.* $\left|\frac{\partial S}{\partial \sigma}\right|$ are compared. In the plane $d_s - \sigma$, the parabola $d_s = \sigma - \sigma^2$ is the locus where both parameters have the same influence on the outcome. If $d_s < \sigma - \sigma^2$, then $\left|\frac{\partial S}{\partial d_s}\right| > \left|\frac{\partial S}{\partial \sigma}\right|$. Sexuals should try to resist perturbations rather than move to new territory. If $d_s > \sigma - \sigma^2$, then $\left|\frac{\partial S}{\partial d_s}\right| < \left|\frac{\partial S}{\partial \sigma}\right|$. This means that colonisation becomes more important than persistence. Other examples of the kind of conclusion that this model allows to draw follow. First, if it is assumed that sexually produced progeny are better adapted to environmental challenges, due to their genetic diversity, but that both morphs disperse equally, this may be translated into $\alpha > \sigma$ and $d_s = d_a$. $1 - \mathcal{S}$ will always be greater than $1 - \mathcal{A}$. That is, the occupancy of sexuals is favoured. Second, if sexuals are considered better dispersers and morphs are not assumed to differ in their ability to cope with the environment, that is, $d_s > d_a$ and $\alpha = \sigma$, then $1 - \mathcal{A} < 1 - \mathcal{S}$. Sexuals are stronger on the territory. This discussion of the results of the models are in accord with those of authors that suggest that environmental uncertainty may positively affect species richness in an ecosystem (Dayton and Hessler, 1972; Connell, 1978; Chesson, 1985; Caswell and Cohen, 1991a, 1991b). The nature of this environmental uncertainty is not given in the parameters of the model. Mortality may be due to senescence leading to natural death, or to the action of external biotic and abiotic factors. Should the model be useful to study a given ecosystem, then it will be up to the researcher implementing it to decide what the values of α and σ are and what the included disturbances represent.

The inclusion of male function in the patch-occupancy model has proved the robustness of the results of the two first, simpler models. Both stable and unstable coexistence are possible, even under more realistic biological conditions, which could have rendered the previous results fragile. Overall, the new patch-occupancy approach has already shown how drastically results can change when spatial considerations are made. It reinforces the idea that different spatial aspects of the biological situation under study, the coexistence of sexual and asexual forms in populations of angiosperms, must be included in modelling attempts. This new model, however, is not fully comprehensive. After all, a patch occupancy model introduces space in an implicit way. The analysis of spatially explicit models could further help in the study of populations mixed for reproductive mode because neighbour interactions and realistic distributions of propagule dispersal are other key features of the biological situation being investigated. These aspects of the problem will be undertaken by the models that comprise the rest of this thesis.

Appendix: Proof of consistency of the patch-occupancy model

This small appendix contains the details of the proof of the fact that the mathematical framework proposed to deal with the introduction of space, that is, the representation of the habitat by an infinite number of patches which may be empty, occupied by a sexual or by an asexual individual, is consistent.

Proposition. Let

$$\Omega := \{(p_0, p_s, p_a) |\ 0 \leq p_0 \leq 1, 0 \leq p_s \leq 1, 0 \leq p_a \leq 1;\ p_0 + p_s + p_a = 1\}.$$

Then, the set Ω is invariant under $A(\mathbf{p}(t))$. That is, for any $\mathbf{p}(t) \in \Omega$, the vector $\mathbf{p}(t+1) = A(\mathbf{p}(t))\mathbf{p}(t)$ belongs to Ω.

Proof.

$$\mathbf{p}(t+1) = A(\mathbf{p}(t))\mathbf{p}(t)$$

$$= \begin{pmatrix} 1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha) & \sigma & \alpha \\ C_s(1-\sigma)(1-C_a) & 1-\sigma & 0 \\ C_a(1-\alpha) & 0 & 1-\alpha \end{pmatrix} \begin{pmatrix} p_0(t) \\ p_s(t) \\ p_a(t) \end{pmatrix}$$

$$= \begin{pmatrix} (1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha))p_0(t) + \sigma p_s(t) + \alpha p_a(t) \\ C_s(1-\sigma)(1-C_a)p_0(t) + (1-\sigma)p_s(t) \\ C_a(1-\alpha)p_0(t) + (1-\alpha)p_a(t) \end{pmatrix}.$$

Addition of the entries of this vector gives

$$\begin{gathered} (1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha))p_0(t) + \sigma p_s(t) + \alpha p_a(t) \\ + C_s(1-\sigma)(1-C_a)p_0(t) + (1-\sigma)p_s(t) \\ + C_a(1-\alpha)p_0(t) + (1-\alpha)p_a(t) \\ = p_0(t) + p_s(t) + p_a(t) = 1 \end{gathered}$$

since $\mathbf{p}(t) \in \Omega$. Moreover,

$$p_0(t+1) = (1 - C_s(1-\sigma)(1-C_a) - C_a(1-\alpha))p_0(t) + \sigma p_s(t) + \alpha p_a(t),$$

$$p_s(t+1) = C_s(1-\sigma)(1-C_a)p_0(t) + (1-\sigma)p_s(t),$$

and

$$p_a(t+1) = C_a(1-\alpha)p_0(t) + (1-\alpha)p_a(t).$$

These three numbers are positive because they are made up of sums of products of positive numbers. The fact that the three of them add up to one implies that none of them is greater than one. Therefore, $\mathbf{p}(t+1) \in \Omega$. ■

Chapter 4

Local Ecological Interactions in a Cellular Automaton Model

The model for temporal dynamics of a mixed population presented in chapter 2 follows traditional ecological population models seeking equilibria and analysing stability of a system of difference equations. The interaction between sexual and asexual individuals is basically a mass action law and the main underlying assumption is that the system is "well mixed". However, in many biological situations, this assumption does not hold. For example, a plant population may not have an apparent spatial structure, but it is definitely not a well-mixed system: individuals do not move around, many plants reproduce (at least partly) vegetatively and even seeds often do not disperse far (van Baalen and Rand, 1998). It is not a new insight that spatial structure is often an essential component of the ecological and evolutionary dynamics of populations, and there have been many approaches to understanding the various consequences of spatial structure (van Baalen, 2000). In order to introduce spatial considerations in this research, chapter 3 presented the oldest of such approaches: implicit introduction of space in a patch-occupancy or metapopulation model (also referred to as a mean-field model, as will be seen later). The model followed the pattern set by Levins (1969, 1970) and Cohen (1970), by considering a population inhabiting an (infinite) array of discrete patches. Space, however, often has a more continuous aspect and subdivisions, although not sharp, are created by restricted movement. This corresponds to what Hamilton (1964) named a "viscous population" (van Baalen, 2000). In a population of plants, where mobility and dispersal are limited, it is extremely important to explicitly consider the spatial pattern of individuals when predicting population dynamics (Iwasa, 2000).

Cellular automaton models are useful for modelling spatially structured populations. A cellular automaton is an array of cells (lattice), each of which may be in one of a finite number of states (*e.g.* empty/occupied). For a population of plants it seems natural to consider a two-dimensional square lattice, but other shapes and dimensions could also be used, for example a lattice of hexagons or tetrahedrons. The state of the entire cellular automaton is given by the configuration of cell states. It is discrete in time and at each time step each cell may change state according to its own state and that of nearest-neighbouring cells, following a predetermined function or transition rule. The simplest cellular automata have deterministic transition rules that are identical for all cells. Stochastic and heterogeneous cellular automata may be better suited to ecological applications. In the most complicated automata, the number of nearest neighbours considered may change from one cell to another (von Neumann, 1966; Caswell and Etter, 1993; Rand et al., 1995; Deutsch, 2000; van Baalen, 2000). Cellular automata are relatively novel in Biology, but the growing interest in spatial issues has lead to their varied uses in models of pigmentation patterns, interspecific competition, host-parasitoid interactions, clonal growth in plants and forest gap dynamics. For reviews on the use of cellular automata in Biology, see Ermentrout and Edelstein-Keshet (1993), Caswell and Etter (1993), Dieckmann *et al.* (2000) and Deutsch and Dormann (2002). Keeling and Rand (1995) have studied the spatial mechanisms of parasite-mediated coexistence of sexual and asexual forms in animals using a lattice model.

Space has become, indeed, the predominant factor of both empirical and theoretical studies to understand, for instance, how localisation of competition and range of dispersal play a role in the dynamics of a population (Tilman and Kareiva, 1997; Hiebeler, 1997; Neuhauser, 2001). In the ecology of flowering plants, local interactions are of the outmost importance. Thus, explicit spatial models such as cellular automata (referred to as CA) will be the most adequate tool to take this research forward. Moreover, CA are intrinsically related to patch-occupancy models (PO) such as the one used in the previous chapter. In fact, to construct an ecological CA model is to translate a set of ecological hypotheses into a set of CA transition rules. The approach to constructing PO models can be applied directly to CA models by defining the colonisation probabilities in terms of local species frequencies (*i.e.* the frequencies in the immediately neighbouring cells) rather than in terms of the global occurrence of the species. This permits a comparison of the results of the CA model and the corresponding mean-field (MF) model (Caswell and Etter, 1993), as shall be seen later, when analytic approximations are implemented. In particular, for hermaphrodites whose asexual descendants have retained male function and coexist with their sexual counterparts, local interactions between sexual and asexual individuals should be reflected in the rules of an explicit spatial model. This is one of the advantages of the CA approach: being spatially explicit, CA include more information and their expression in terms of transition rules lays bare the factors determining the dynamics (Caswell and Etter, 1993).

Having retained a hold on sexuality via the male function, asexuals may compete with sexuals to fertilise sexual eggs, making asexuals potential male parents. Due to polyploidy, however, pollen produced by asexuals may be sterile or it may lead to post-zygotic seed abortion (Norrmann *et al.*, 1994). Nevertheless, asexuals are also able to produce at least some viable and effective male gametes (Richards, 1973; Morita *et al.,* 1990). All else being equal, if asexuality resulted in the loss of male function, there would be no cost of sex in hermaphrodites (Charlesworth, 1980). Consequently, male function in asexuals is a key factor in the study of sexuality *vs.* asexuality. This implies important spatial considerations: a closer look into pollen dispersal mechanisms quickly discards random mating as a modelling assumption. Dispersed by pollinators such as insects, pollen has a limited radius of action. Insects move from one flower to its near neighbours (Bertin, 1988), which in terms of paternity means that most insect-pollinated flowering plants interact successfully with a limited number of pollen donors. Meagher (1986) gives an estimate of less than six actual mates per individual in the willow herb *Chamaelirium luteum.* The importance of nearest-neighbour pollination for the genetic differentiation of populations with this type of breeding system has been discussed by Turner *et al.* (1982). The dynamics of pollen dispersal just described point in the direction of strong neighbour effects. This reinforces the argument that cellular automata are the most appropriate modelling tool to investigate the role of local interactions in the possible coexistence of sexual and asexual reproduction.

4.1 The model

As before, a population of flowering plants that are simultaneous hermaphrodites will be considered. It is assumed that asexuality arises from a mutation as a dominant trait in a population originally comprising only sexual (s) individuals. Plants that carry the mutant gene (a), and that will be referred to as asexuals, have a modified female function that produces eggs that develop into new individuals without any need for fertilisation. Moreover, they have also retained some level of male function. Therefore, the population consists of a mixture of sexual and asexual individuals. Other previous assumptions also hold: sexual and asexual individuals allocate the same fraction of their resources to male and female function, denoted k_m, $0 < k_m$, and k_f, $0 < k_f$, respectively. Male function in asexuals may not be completely efficient. A fraction u, $0 \leq u \leq 1$, of the pollen produced by asexuals will be sterile and will not compete with viable pollen for eggs. Another fraction b, $0 \leq b \leq 1$, will lead to post-zygotic seed abortion. As for the rest of the pollen, a fraction g_s, $0 \leq g_s \leq 1$, of the pollen produced by asexuals is viable and carries a gene s for sexuality; a fraction g_a, $0 \leq g_a \leq 1$, is viable and carries a gene a for asexuality (usually $g_s = g_a$). $u + b + g_s + g_a = 1$, although from now on it will be assumed that $b = 0$, for simplicity only. Viable pollen produced by asexuals may be of the same quality as pollen produced by sexuals. The population is supposed to be spread over a two-dimensional square lattice, with at most one individual per cell. Cells may be in one of three states: empty, occupied by a sexual individual or occupied by an asexual individual. The nearest neighbours of a given cell are those in the Moore neighbourhood —the eight closest cells— around it. In each time step, the following processes take place:

(1) Reproduction: each sexual invests some of its resources to produce k_f eggs which may be fertilised by the pollen produced by its eight nearest neighbours. If a cell in the lattice has coordinates (i, j), the number of sexuals among its nearest neighbours is denoted as $n_s(i, j)$ and the number of asexual nearest neighbours as $n_a(i, j)$. These nearest neighbours will produce a total of $k_m(n_s(i, j) + (1 - u)n_a(i, j)) = \bar{m}$ viable male gametes, where $\bar{m}$ is the sum of the numbers of male gametes from all nearest neighbours, weighted by the viability of their pollen. $k_f \frac{n_s(i,j)}{\bar{m}}$ of the sexual eggs are fertilised by pollen produced by other sexuals in the neighbourhood, $k_f \frac{g_s n_a(i,j)}{\bar{m}}$ are fertilised by pollen carrying gene s produced by asexual nearest neighbours and $k_f \frac{g_a n_a(i,j)}{\bar{m}}$ are fertilised by pollen carrying gene a produced by asexual nearest neighbours. The first two types of fertilised eggs will produce seeds (or propagules) carrying sexual embryos whereas the last type will carry asexual embryos, regardless of the fact that they were all sexually produced. In addition to these sexually produced offspring, each asexual individual also produces k_f eggs that develop into new asexual individuals without fertilisation, sometimes referred to as clones. So far, offspring are being considered according to their own reproductive mode and not to that of their parents. However, the sexual or asexual origin of the offspring does have an effect on how these reach maturity. It will be assumed that all sexually produced offspring have a viability

v_s, $0 \leq v_s \leq 1$, due to their sexual origin, while a viability v_a, $0 \leq v_a \leq 1$, will be assigned to purely asexually derived offspring. When $v_s > v_a$, this model is in accord with models that assume that offspring with recombined genomes may be at an advantage over those that have received a copy of the maternal genome (Hurst and Peck, 1996). Thus, at maturity, there will be $v_s k_f \frac{n_s(i,j)+(g_s+g_a)n_a(i,j)}{\bar{m}} = v_s k_f$ sexually derived offspring and $v_a k_f$ asexual clones produced per asexual individual.

To sum up, there are four types of progeny according to their origin, but only two according to their phenotype. Their numbers at maturity are given as follows:

$$n_{ss} = v_s k_f \frac{n_s(i,j)}{\bar{m}}, \tag{4.1}$$

$$n_{sx} = v_s k_f \frac{g_s n_a(i,j)}{\bar{m}}, \tag{4.2}$$

$$n_{ax} = v_s k_f \frac{g_a n_a(i,j)}{\bar{m}} \tag{4.3}$$

and

$$n_{aa} = v_a k_f. \tag{4.4}$$

In these equations, n_{po} denotes the number of progeny of phenotype p and origin o. Within this notation, x represents a cross between individuals with different reproductive modes. It is important to notice that n_{aa} is the same for all asexual individuals in the lattice but n_{ss}, n_{sx} and n_{ax} depend on the sexual individual producing the eggs that are fertilised and the numbers $n_s(i,j)$ and $n_a(i,j)$ among its nearest neighbours.

(2) Colonisation: an empty cell will be colonised by the propagules produced by its eight nearest neighbours. It is assumed that colonisation is given by a Poisson process at a rate $d_s\bar{p}_s + d_a\bar{p}_a$, where $\bar{p}_s$ and $\bar{p}_a$ are local frequencies of sexual and asexual propagules defined formally below. An empty cell remains so if neither a sexual nor an asexual propagule colonises it. In mathematical terms, the probability that an empty cell remains empty is given by $C_0 = \mathrm{e}^{-(d_s\bar{p}_s+d_a\bar{p}_a)}$. A propagule chosen at random colonises an empty cell. The probability that an empty cell is colonised by a sexual propagule is given by $C_s = \frac{d_s\bar{p}_s}{d_s\bar{p}_s+d_a\bar{p}_a}(1 - C_0)$ and the probability that it is colonised by an asexual propagule is given by $C_a = \frac{d_a\bar{p}_a}{d_s\bar{p}_s+d_a\bar{p}_a}(1 - C_0)$. The parameters d_s and d_a are the dispersal coefficients

of sexual and asexual propagules respectively. These positive numbers could be different but for simplicity our examples of simulations use $d_s = d_a = 1$. As mentioned before, the variables $\bar{p}_s$ and $\bar{p}_a$ are the proportions of sexual and asexual propagules produced in the neighbourhood of the empty cell. These proportions are given by the following equations:

Let $S(i,j)$ denote the set of all sexual nearest neighbours of an empty cell at location (i,j) in the lattice. Similarly, $A(i,j)$ will denote the set of asexual nearest neighbouring cells of (i,j). Then

$$\bar{p}_s = \frac{\sum_{s\in S(i,j)} n_{ss}(s) + \sum_{s\in S(i,j)} n_{sx}(s)}{\sum_{s\in S(i,j)} n_{ss}(s) + \sum_{s\in S(i,j)} n_{sx}(s) + \sum_{s\in S(i,j)} n_{ax}(s) + \sum_{a\in A(i,j)} n_{aa}(a)}$$

and

$$\bar{p}_a = \frac{\sum_{s\in S(i,j)} n_{ax}(s) + \sum_{a\in A(i,j)} n_{aa}(a)}{\sum_{s\in S(i,j)} n_{ss}(s) + \sum_{s\in S(i,j)} n_{sx}(s) + \sum_{s\in S(i,j)} n_{ax}(s) + \sum_{a\in A(i,j)} n_{aa}(a)}.$$

These are the local proportions of sexual and asexual propagules produced around an empty cell. Therefore, they are different for each empty cell in the lattice.

(3) Disturbance: individuals occupying cells cannot be displaced by other individuals or propagules and will abandon a cell only after removal. This may happen as a result of natural death or by action of disturbances affecting the landscape. The probability that a cell occupied by a sexual becomes empty is given by σ, $0 \leq \sigma \leq 1$, whereas the probability that a cell occupied by an asexual becomes empty is given by α, $0 \leq \alpha \leq 1$. Disturbances occur independently for each cell and their probabilities of occurrence are constant over time and equal for all cells.

4.2 Analysis of the automaton

It is well known that most cellular automata resist analytical study and are capable of exhibiting amazingly complex behaviour (Wolfram, 1983). Thus, the model has first been studied through numerical simulations before attempting any analytical approach. An initial landscape with a uniform distribution of empty, sexual and asexual cells and periodic boundary conditions is updated every generation according to the transition rules described above. A typical initial-condition landscape produced by the program is shown in figure 4.1. Decisions

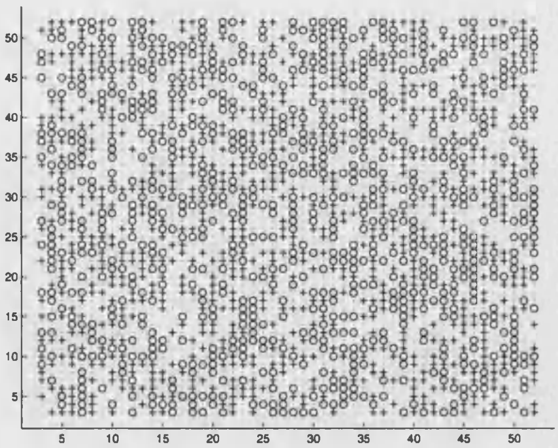


Figure 4.1: A typical initial condition generated by a program that simulates the CA. The distribution of empty ( ), sexual (o) and asexual (+) cells is uniform. For visual clarity a 50 × 50 grid is shown, but simulations were run using 225^2 points.

behind the creation of the initial landscape and the application of updating rules rely on a random number generator. This makes the proposed CA completely stochastic.

Every generation the number of cells in each state was recorded. This assumes that an individual produces seeds in the year that it germinates, with these seeds germinating in the following year. This pattern of reproduction is exhibited by many apomictic herbs, including *Taraxacum* species, but not by apomictic trees, in which reproductive maturity occurs several years after germination. The automaton ran for 15,000 generations, which equates with a period of time that greatly exceeds the length of the present interglacial period, estimated at *c.* 10,000 years (Forsstrom, 2001), and which approximates to the length of the preceding interglacial period (Cox and Moore, 1993: 259-271). Repeated runs of the program for different values of the parameters involved (g_s, g_a, u, $\mu = \frac{v_s}{v_a}$, σ, α, d_s and d_a) consistently showed that the system goes to fixation of one of the reproductive modes in the landscape. Spatial aggregation of individuals into sexual or asexual clumps was also observed. According to different choices of parameter values, fixation or extinction of one of the reproductive modes can take place within a few generations, or both modes may have a strong presence after several thousands of generations, as shown in figure 4.2. The example provided in figure 4.2 (middle) does not contradict the initial statement that the CA goes to fixation of one of the two morphs. If allowed to run for longer than the interglacial period, something that is beyond the aims of this model, fixation, of sexuals in this case, would be obtained. However, examples like this, where both reproductive modes appear throughout the interglacial period, both with strong presence, are instances of coexistence in the biological sense.

To summarise the information given by different runs of the CA, a disturbance parameter space is obtained varying only σ and α with all other parameters fixed. For instance, the choice $g_s = g_a = 0.25$, $u = 0.5$, $\mu = 1$, and $d_s = d_a = 1$ sets a stage with no built-in advantages for either sexuals or asexuals. The differences between them will be given by changes in their mortality rates σ and α. On the corresponding $\sigma - \alpha$ plane shown in figure 4.3, it is possible to distinguish a region where sexuals go to fixation and a region where asexuals prevail. Due to the stochasticity of the model, every $\sigma - \alpha$ combination demands several repetitions of the experiment to identify the trend shown in the map of results. In their numerical experiments, Turner *et al.* (1982) suggest a minimum of 10. To run this model, 20 to 100 where used, according to the proximity to the border between sexual and asexual fixation. As the simulations approach the interface between the sexual and asexual regions, the times to fixation increase. This can be seen in the same figure. These times to fixation also vary for different runs because of the stochasticity of the CA, but they are always much greater closer to the interface, independently of the repetitions of the experiment for a given combination of parameters. The same behaviour can be observed for other selections of parameters. Figure 4.4 shows the results over a $\sigma - \alpha$ plane and times to fixation for $g_s = g_a = 0.25$, $d_s = d_a = 1$, $u = 0.5$ and $\mu = 5$, a combination of parameters that yields stable coexistence of both types in the mean field model presented in section 3.1.

In order to analyse the results obtained, some tests were performed on the data. First, a chi-squared test confirmed that the mingling of empty, sexual and asexual cells was not random except for the initial landscape and perhaps for a few following generations. The second test to be applied was a generalised runs test. Pielou (1977) describes a technique used in field ecology to test for the spatial aggregation of individuals of the same species in a habitat where two species, A and B, are present: a line or transect is traced across the habitat. The sequence of individuals of species A or B encountered along this transect is recorded. An uninterrupted subsequence of As or Bs is called a run. Once the number of runs in the transect has been found, it is then possible to calculate the probability of finding this number of runs in any given transect. This technique, called a runs test, provides a measure of spatial aggregation. To analyse the data produced by the CA, a generalisation of this procedure was implemented. Each row and column was used as a transect and the number of runs per transect was recorded. The mean number of runs per transect was used as a description of the landscape.

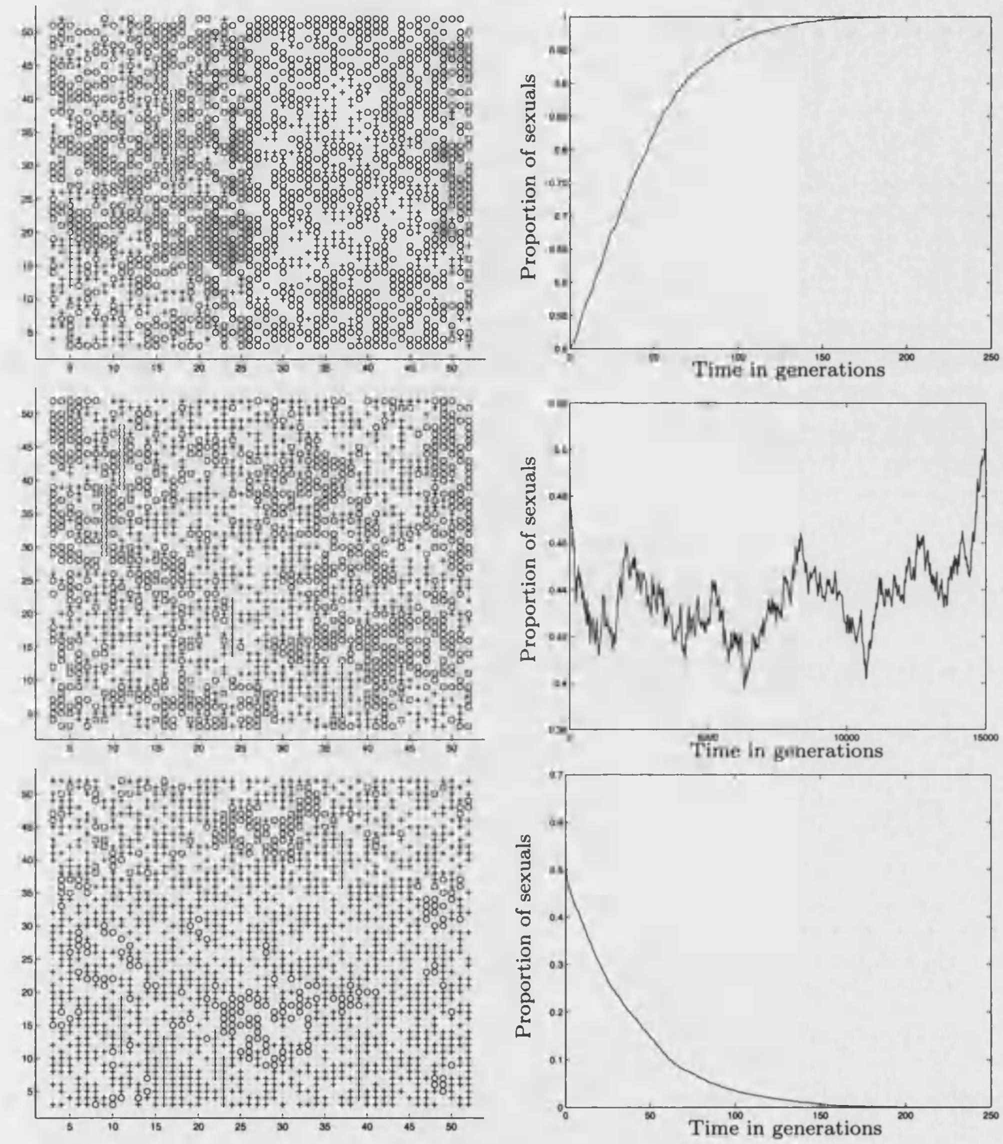
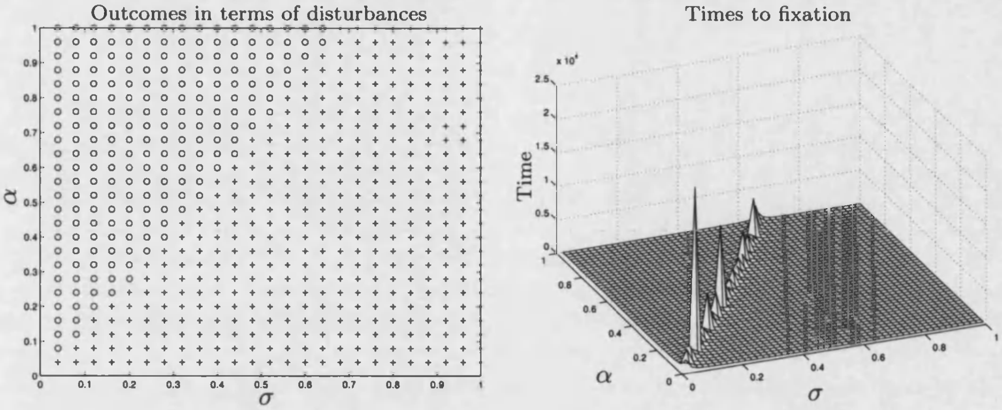
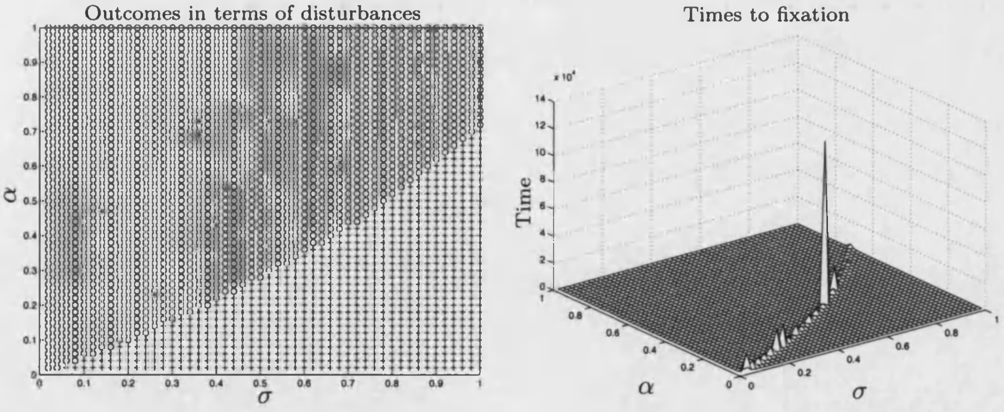


Figure 4.2: Fixed parameter values are $d_s = 1$, $d_a = 1$, $g_s = g_a = 0.25$, $u = 0.5$, and $\mu = 1$. Top: for $\sigma = 0.25$ and $\alpha = 0.4$, the landscape shows clear dominance of sexuals (o) after only 50 generations. They go to fixation in 213 generations, as shown by the proportion of sexuals $\frac{N_s}{N_s+N_a}$ graphed against time (in generations) to the right. Middle: the left panel shows a snapshot of the landscape for $\sigma = 0.25$ and $\alpha = 0.3486$. This is a choice of parameters closer to the sexual-asexual interface along the line $\sigma = 0.25$. In this case both modes have a strong presence through the 15,000 generations of the simulation. Bottom: with mortality rates $\sigma = 0.25$ and $\alpha = 0.3$ asexuals (+) are dominant and drive sexuals out of the landscape in 246 generations. All cases give evidence for the formation of clusters.


Outcomes in terms of disturbances

Times to fixation

Figure 4.3: Map of results over a disturbance parameter space where fixed parameters are $d_s = d_a = 1$, $g_s = g_a = 0.25$, $u = 0.5$, and $\mu = 1$. As the simulation approaches the interface between the regions for sexual(o) and asexual(+) fixation, the time to completion increases (right). This corresponds to longer coexistence periods before fixation occurs.


Outcomes in terms of disturbances

Times to fixation

Figure 4.4: Map of results over a disturbance parameter space where fixed parameters are $d_s = d_a = 1$, $g_s = g_a = 0.25$, $u = 0.5$, and $\mu = 5$. As in other examples, times to fixation increase as the simulation approaches the interface between the sexual(o) and asexual(+) regions. Longer coexistence periods are observed.

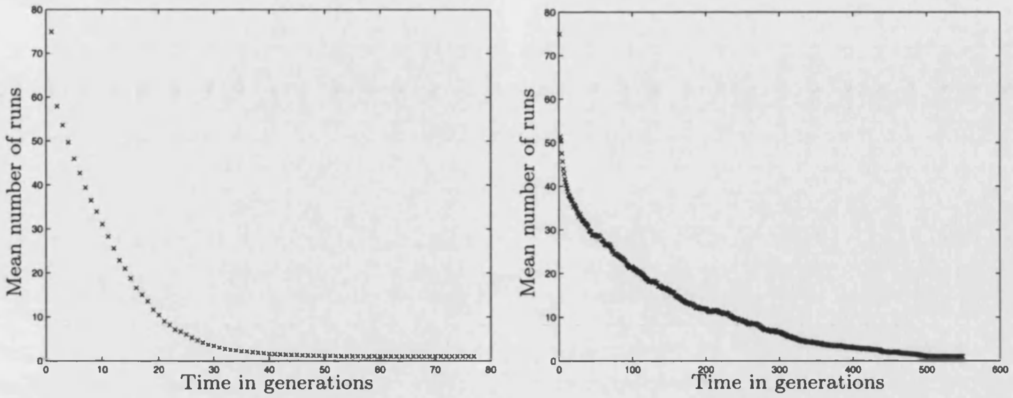


Figure 4.5: Mean number of runs against time (in generations). Fixed parameter values are $d_s = 1 = d_a = 1$, $g_s = g_a = 0.25$, $u = 0.5$, $\mu = 1$ and $\sigma = 0.5$. The graph to the right shows a simulation closer to the interface ($\alpha = 0.7$), while the figure to the left was produced with $\alpha = 0.5$, showing shorter fixation and coexistence periods.

In a habitat where sexual and asexual individuals are randomly mixed, such as the initial condition landscape of each numerical simulation, this number is expected to be $\frac{1}{3}N + \frac{1}{2}$ for the initial conditions used here and $N = 225$. If spatial aggregation is observed, the number will decrease as the landscape changes. If the final outcome of the dynamics of the population in the habitat is fixation, then this number will tend to 1, since only one reproductive mode remains in the landscape. However, it is possible to arbitrarily define a coexistence range and study the number of generations the landscape remains within this coexistence range. Again, this coexistence period is extended for values of parameters close to the interface between the regions of sexual and asexual dominance. To illustrate the use of the modified runs test, figure 4.5 shows the mean number of runs per generation for two different simulations, one of which is closer to the sexual-asexual interface.

Finally, cluster analysis was implemented on the data produced by the CA. Following Zupan (1982), the distances between all points of a same type, for example all sexuals, in a landscape were measured in order to find those two elements which were 'closest' neighbours using pairwise Euclidean distances all over the landscape. These were then grouped into an object whose coordinates are the average of the coordinates of the selected elements. This was repeated for all elements and objects obtained in the first step. The increasing sequence of smallest distances thus obtained was halted when a maximal distance was reached. This maximal distance also gives a measure of cluster size or neighbourhood radius. Once this process was interrupted, the number of clusters at that moment and the number of elements per cluster were noted. Using this analysis, the results obtained consistently showed a decreasing number of clusters and an increasing number of elements per cluster, which indeed points to spatial aggregation between elements of the same kind. These results are in accordance with evidence for development and persistence of patches in the spatial distribution of genotypes in a population with nearest-neighbour pollination found by Turner *et al.* (1982).

All three tests have confirmed the original observations about the CA behaviour. However, in order to be able to draw more general conclusions, it is necessary to implement some analytical techniques.

4.3 Analytic approximations

If the ease of simulation is one of the advantages of using a cellular automaton, the difficulty of its analysis, other than by direct computer simulations, is one of the main drawbacks of this choice of model. In the words of van Baalen (2000: 361):

> It is relatively straightforward to model a spatial ecological system by setting up a lattice of sites and defining a set of rules that change the state of sites depending on their state and that of their environment. The advantage of this approach is that spatial phenomena are explicitly included. A disadvantage, however, is that simulating these models is rather time consuming. More seriously, the results are sometimes difficult to interpret and are not easily generalised.

This difficulty has prompted many researchers to look for ways of analysing results of a CA model. Most of the techniques developed so far emerged from statistical mechanics of physical systems, but it was soon obvious that they could also be applied to biological systems. The implementation of this kind of analysis somehow relies on the assumption that “space doesn’t matter” and effectively takes the modeller back to an implicit spatial approach (Hiebeler, 1997; van Baalen and Rand, 1998). There are many ways to implement analytic studies, as will be shown in the following sections.

4.3.1 Mean-field approximation

Mean field approximations are widely used to obtain macroscopic equations from cellular automaton rules (Deutsch, 2000). In these approximations, the study of the dynamics of an array of cells is transformed into the study of a set of equations describing the changes in the proportion of cells in each state (Caswell and Etter, 1993). Mean field approximations are averaged simplifications of a CA where space is normally made implicit either by allowing for dispersal over arbitrarily long distances or by ignoring the spatial correlations that develop in the lattice over time (Hiebeler, 1997). In this case, the corresponding mean field approximation is obtained when both fertilisation and colonisation are assumed to take place all over the landscape, not just locally.

Under this assumption, the mean field approximation to the CA is given by the following system of equations:

$$\frac{dp_s}{dt} = C_s(1 - p_s - p_a) - \sigma p_s \tag{4.5}$$

and

$$\frac{dp_a}{dt} = C_a(1 - p_s - p_a) - \alpha p_a, \tag{4.6}$$

where C_s and C_a are defined as in the local transition rules, but with p_s and p_a taken as global proportions of cells in state s and a respectively. This new model is very similar to the PO model studied in chapter 3. Although we are in fact going from the CA back to the PO approach, in a sort of inverse algorithm to that suggested by Caswell and Etter to build a CA model from a PO model, the equations are not exactly the same. In this first spatially explicit model, asexuals were not given the advantage of being better colonisers. Therein lies the difference between the PO model in the previous chapter and this mean-field approximation to the CA model. It can be seen that the conditions to obtain stable coexistence in the mean field approximation (4.5)–(4.6) to the CA are given by

$$\sigma < \frac{d_s \mu g_s}{d_a(1-u)}\alpha,$$

and

$$\sigma > \frac{d_s \mu}{d_a(\mu g_a + 1)}\alpha.$$

On the other hand, conditions for fixation are given by

$$\sigma > \frac{d_s \mu g_s}{d_a(1-u)}\alpha,$$

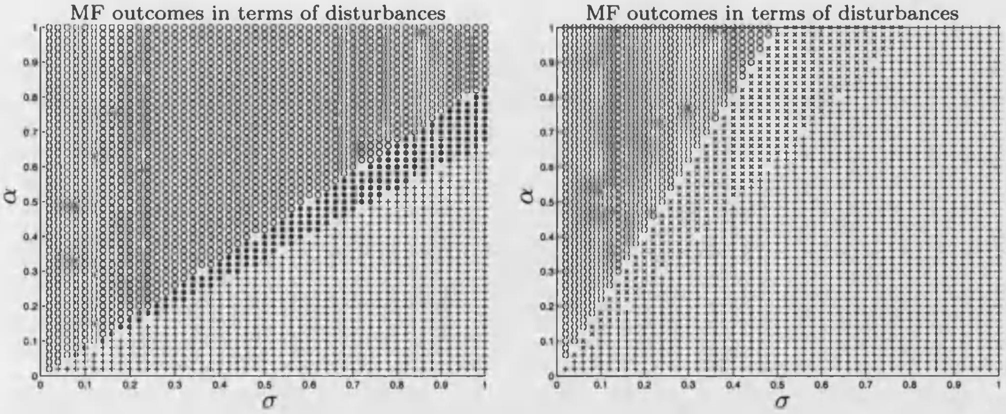


Figure 4.6: Example of disturbance parameter spaces for the mean field model. Left: Stable coexistence (*) is obtained using parameters $d_s = 1$, $d_a = 1$, $g_s = g_a = 0.5$, $u = 0$ and $\mu = 3$. (o) stands for sexual and (+) for asexual fixation, respectively. Right: With $\mu = 1$, the mean field model presents a region of unstable coexistence (x).

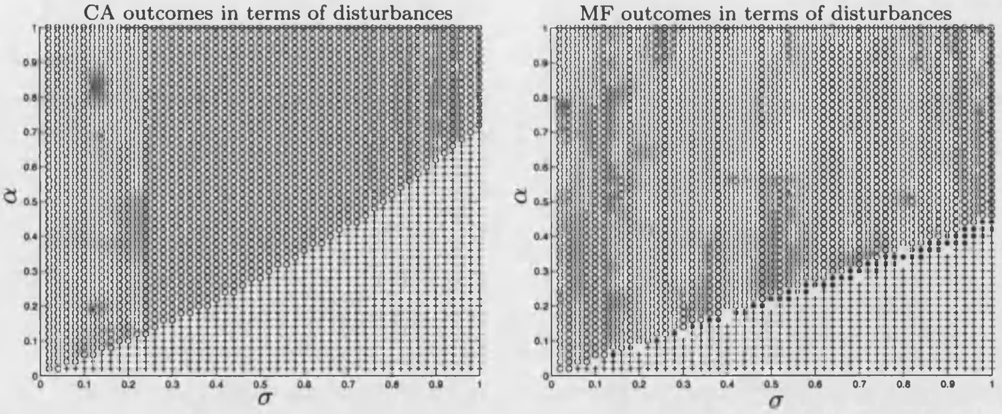
and

$$\sigma < \frac{d_s \mu}{d_a(\mu g_a + 1)} \alpha.$$

These conditions describe lines in the disturbance parameter spaces shown in figure 4.6. As in the CA, regions of sexual or asexual fixation are clearly identified. However, for certain choices of parameter values, the mean field approximation allows for stable coexistence. Figure 4.7 shows simulations of the CA over a $\sigma - \alpha$ parameter space using $d_s = d_a = 1$, $g_s = g_a = 0.25$, $u = 0.5$ and $\mu = 5$ in contradistinction to the same outcome space for the mean field approximation. The stable coexistence region that was observed for the mean field approximation has disappeared. Where the mean field approximation exhibited coexistence, the CA gives fixation of asexuals. This contrast appears in all other comparisons of the CA and its mean field approximation when the latter exhibits stable coexistence. Therefore, the behaviour of the CA and its corresponding mean field approximation are qualitatively different.

4.3.2 Correlation dynamics

Mean-field approximations are exact when the pattern created by a spatially explicit model is random. However, when ecological and demographic processes are limited, spatially explicit models result in characteristic spatial patterns in which individuals of the same type tend to form clumps. In this case, local densities may be much higher than global densities and track is to be kept of both



CA outcomes in terms of disturbances

MF outcomes in terms of disturbances

Figure 4.7: Example of the contrasting behaviour of the CA and its mean field approximation. With parameters $d_s = d_a = 1$, $g_s = g_a = 0.25$, $u = 0.5$ and $\mu = 5.$, the mean field approximation (right panel) shows stable coexistence (*), an outcome that is not possible in the CA (left panel).

local and global quantities. In order to accomplish this, it is possible to consider minimal structures larger than that of a single site. Also, the correlations between the elements of the alternative basic structure should be taken into account. Hence the name of the techniques that follow: correlation-dynamics studies.

Local structure

Sometimes referred to as local-dispersal mean-field approximation, this technique ignores space not by assuming dispersal over arbitrarily long distances in the lattice, but by leaving dispersal restricted to nearest-neighbouring cells, as it is in the original CA model, and instead assuming that no spatial correlations between sites develop in time. This is not true of a model with local interactions, but allows the state of cells to be considered as independent of one another, and thus allows the probability of observing a certain configuration to be calculated as the product of the probabilities of occurrence of the states of each cell in the configuration. The basic structure chosen here is a given cell and its nearest neighbours. For the CA under study, this implies a basic structure of 25 cells which may be in any of 25^3 configurations. Although this seems a prohibitively high number of configurations to be analysed, this set can be broken into three subsets, according to the state of the central cell (s, a or 0) and then the probability can be sought of this central cell changing state given a certain configuration. That is, one wants to find the probability of finding a particular site in state i at time $t+1$ by conditioning on the state of the pre-image of that site at time t. This probability is given by the expression

$$P_{t+1}[i] = \sum_{g \in G} P_t[g] P[g \text{ produces a site in state } i],$$

where G is the set of all possible configurations of the pre-image structure. Notice that because of the assumption that no correlations develop in time, $P_t[g]$ is simply given by $p_s^{\#_s(g)} p_a^{\#_a(g)} p_0^{\#_0(g)}$, where $\#_i(g)$ is the number of sites in state i in the pre-image g. Symmetries in the 24-cell neighbourhood around a given site allow for further reduction in the number of configurations to be considered. Still, the number of calculations is high and has to be done by a computer. These simulations take up to two days to sweep the whole 225^2-cell landscape. They may underestimate the actual local densities of sexual, asexual and empty sites because of the assumption that no correlations develop. Even though this technique relies on assuming that no correlations develop in time, and therefore it does not seem to fit in the current section of this work about correlation dynamics, next it will be seen how the information it produces is valuable when implementing correlation studies. For a detailed discussion of the local-dispersal mean-field approximation see Hiebeler (1997).

Pair approximation

A step up into analytic techniques to study a CA model is to generalise the local-dispersal mean field technique described above. This time, correlations between sites in the lattice will be considered. The simplest structure in which a correlation may develop is a pair of neighbouring sites, hence the name of this new technique: pair approximation. It was developed by Matsuda *et al.* (1992) to study lattice models. It is a system of differential equations that yields average densities and local densities, with the latter describing the correlation of states of pairs of nearest-neighbour cells. Pair approximations are capable of predicting the behaviour of lattice models even when mean-field approximations fail (Harada and Iwasa, 1994; Sato *et al.*, 1994; Harada *et al.*, 1995).

In a pair approximation one basically wants to investigate local densities, in addition to the already-known global densities p_s, p_a and p_0. These local densities are the probabilities that a randomly chosen neighbour of a randomly chosen site in the lattice is in state i given that the chosen site is in state j; $i, j \in \{s, a, 0\}$. These probabilities will be denoted as $q_{s/s}$, $q_{a/s}$, $q_{0/s}$, $q_{a/a}$, $q_{s/a}$, $q_{0/a}$, $q_{s/0}$, $q_{a/0}$ and $q_{0/0}$. Together with the global densities, a pair approximation for the CA in this chapter would, in principle, be a system of 12 difference equations, but relations between the quantities under study, such as $p_s + p_a + p_0 = 1$ and $p_{sa} = p_a q_{s/a} = p_s q_{a/s}$, reduces it to only five equations. A methodological note is pertinent here. Pair approximations were originally developed as systems of ordinary differential equations to study lattice models in continuous time (see Iwasa, 2000), but this CA is discrete and thus requires a generalisation of the pair approximation technique developed by Matsuda *et al.* Such generalisations to discrete time have been applied to deterministic cellular automata in physics and, as far as the author is aware, to only one discrete stochastic model in ecology, a one-species model that derives from the models by Caswell and Cohen (see Hiebeler, 1997). Therefore, a pair approximation for a discrete ecological model of this level of complexity has not been tried before. However, in the same way that a pair approximation derives as a system of differential equations from a continuous-time Markov chain (Iwasa, 2000), this one will take the form of a system of difference equations deriving from a discrete-time Markov chain.

Two of the equations, those for the global densities p_s and p_a, in the discrete pair approximation are given by

$$p_s(t+1) = \bar{C}_s(1 - p_s - p_a) + (1 - \sigma)p_s$$

and

$$p_a(t+1) = \bar{C}_a(1 - p_s - p_a) + (1 - \alpha)p_a,$$

where $\bar{C}_s$ and $\bar{C}_a$ are given by

$$\bar{C}_s = 1 - \mathrm{e}^{-(d_s\bar{\bar{p}}_s + d_a)\bar{\bar{p}}_a} \frac{d_s\bar{\bar{p}}_s}{d_s\bar{\bar{p}}_s + d_a\bar{\bar{p}}_a}$$

and

$$\bar{C}_a = 1 - \mathrm{e}^{-(d_s\bar{\bar{p}}_s + d_a)\bar{\bar{p}}_a} \frac{d_a\bar{\bar{p}}_a}{d_s\bar{\bar{p}}_s + d_a\bar{\bar{p}}_a}.$$

In turn, $\bar{\bar{p}}_s$ and $\bar{\bar{p}}_a$ are an "average" over the entire lattice of the local proportions of sexual and asexual progeny used in the CA. They are given by

$$\bar{\bar{p}}_s = \frac{\mu \frac{q_{s/s} + g_s q_{a/s}}{q_{s/s} + (1-u) q_{a/s}} q_{s/0}}{\mu q_{s/0} + q_{a/0}}$$

and

$$\bar{\bar{p}}_a = \frac{q_{a/0} + \mu \frac{g_a q_{a/s}}{q_{s/s} + (1-u) q_{a/s}} q_{s/0}}{\mu q_{s/0} + q_{a/0}}.$$

What has been done is to replace the local quantities n_{ss}, n_{sx}, n_{ax} and n_{aa}, as well as $n_s(i,j)$ and $n_a(i,j)$, by their "averaged" versions $q_{s/s}$, $q_{a/s}$, $q_{s/0}$ and $q_{a/0}$. Thus, the pair approximation is "naturally" calling for an investigation of the behaviour of $q_{s/s}$, $q_{a/s}$, $q_{s/0}$ and $q_{a/0}$. It has been seen, however, that studying three of them is enough, say $q_{s/s}$, $q_{a/s}$ and $q_{a/0}$. By the definition of conditional probability, $q_{s/s} \propto \frac{p_{ss}}{p_s}$, $q_{a/s} \propto \frac{p_{as}}{p_s}$ and $q_{0/s} \propto \frac{p_{s0}}{p_s}$. From the fact that $q_{s/s} + q_{a/s} + q_{0/s} = 1$, it is possible to derive the precise expressions $q_{s/s} = \frac{p_{ss}}{p_s}$, $q_{a/s} = \frac{p_{as}}{2p_s}$ and $q_{0/s} = \frac{p_{s0}}{2p_s}$. In the same way, $q_{a/0} = \frac{p_{a0}}{2p_0}$. Other relations between these quantities give formulas such as $q_{a/0} = q_{0/a}\frac{p_a}{p_0}$. Therefore, the pair approximation can be studied in terms of the quantities p_{ij}, the probabilities that cells of a randomly chosen pair of nearest neighbours are in state ij (or ji). Changes in these quantities are determined as follows:

First consider p_{ss}. From the assumptions of the model it is easy to see that

$$p_{ss}(t+1) = -2\sigma p_{ss} + S_{s/0}(1-\sigma)p_{so} + S_{0/0}^2 p_{00}, \tag{4.7}$$

where σ is the mortality rate of sexuals, $S_{s/0}$ is the probability that an empty patch with at least one sexual neighbour is colonised by a sexual and, similarly, $S_{0/0}$ is the probability that an empty patch with at least one empty neighbour is colonised by a sexual. That the expression in (4.7) derives from the assumptions of the model is verified when one realises that a *ss* pair will cease to be that if either sexual cell changes state, which happens with probability 2σ and thus a total of $2\sigma p_{ss}$ pairs are lost when this happens. A *so* pair becomes *ss* if the empty cell, which has at least one sexual neighbour (that in the pair), is colonised by a sexual propagule ($S_{s/0}$ denotes the probability of this colonisation occurring) and the sexual cell in the pair remains so $(1-\sigma)$. These factors together, the event happens with probability $S_{s/0}(1-\sigma)$ and adds a total of $S_{s/0}(1-\sigma)p_{s0}$ pairs to the count of *ss* pairs in the next time step. Finally, a 00 pair may become a *ss* pair with probability $S_{0/0}^2$, when both empty cells, which have at least one empty neighbour (that of the pair), are colonised by a sexual propagule ($S_{0/0}$). The rules do not allow for changes between states *s* and *a* directly. It is necessary to go through state 0 first, and that takes another time step. The procedure to obtain expressions for the changes in other p_{ij} pairs is completely analogous. Finally, the following discrete Markov chain is obtained:

$$\mathbf{P}(t+1) = A(\mathbf{P}(t))\mathbf{P}(t),$$

with $\mathbf{P}(t) = (p_{ss}(t), p_{sa}(t), p_{s0}(t), p_{aa}(t), p_{a0}(t), p_{00}(t))$ and $A(\mathbf{P}(t))$ the transition matrix

$$\begin{pmatrix}
(1-\sigma)^2 & 0 & (1-\sigma)S_{s/0}S_{0/s} & 0 & 0 & S_{0/0}^2 \\
0 & (1-\sigma)(1-\alpha) & (1-\sigma)A_{s/0} & 0 & (1-\alpha)S_{a/0} & 2S_{0/0}A_{0/0} \\
2(1-\sigma)\sigma & (1-\sigma)\alpha & (1-\sigma)(1-S_{s/0}-A_{s/0})+\sigma S_{s/0} & 0 & S_{a/0}\alpha & 2S_{0/0}(1-S_{0/0}-A_{0/0}) \\
0 & 0 & 0 & (1-\alpha)^2 & A_{a/0}(1-\alpha) & A_{0/0}^2 \\
0 & \sigma(1-\alpha) & \sigma A_{s/0} & 2\alpha(1-\alpha) & (1-\alpha)(1-S_{a/0}-A_{a/0})+\alpha A_{a/0} & 2A_{0/0}(1-S_{0/0}-A_{0/0}) \\
\sigma^2 & \sigma\alpha & \sigma(1-S_{s/0}-A_{s/0}) & \alpha^2 & \alpha(1-S_{a/0}-A_{a/0}) & (1-S_{0/0}-A_{0/0})^2
\end{pmatrix}$$

The numbers $S_{a/0}$, $A_{0/0}$ and $A_{a/0}$ are defined analogously to the definition of $S_{s/0}$ above. This is where the local-dispersal mean field approximation is necessary. These colonisation probabilities have to be calculated using it, as they depend on all possible configurations of the 25-cell neighbourhood. It is not enough that say, the central cell is known to be empty and has at least one empty neighbour. Changing its state from 0 to s, for example, still requires information beyond the average quantities $q_{i/j}$. This is due to the complexity of the CA model and thus it is necessary to rely on computer simulations to study this approximation. Although long, these simulations do provide a better approximation to the CA behaviour than did the mean-field model in section 3.1, as can be seen figure 4.8. The next figure (4.9) shows clearly how for the same parameter values the mean-field model gives stable coexistence where the CA exhibits fixation of asexuals.

4.4 Conclusions

A cellular automaton has indeed proved useful to study the coexistence of sexual and asexual forms. For one thing, it allows the inclusion of detailed local interactions between sexual and asexual individuals, something that has been omitted in previous models. An implicit introduction of space, in the form of a patch-occupancy model such as the mean field approximation presented above, or the models in the previous chapter, assumes perfect mixing and thus gives a very different picture of the phenomenon under study, as is made evident by the

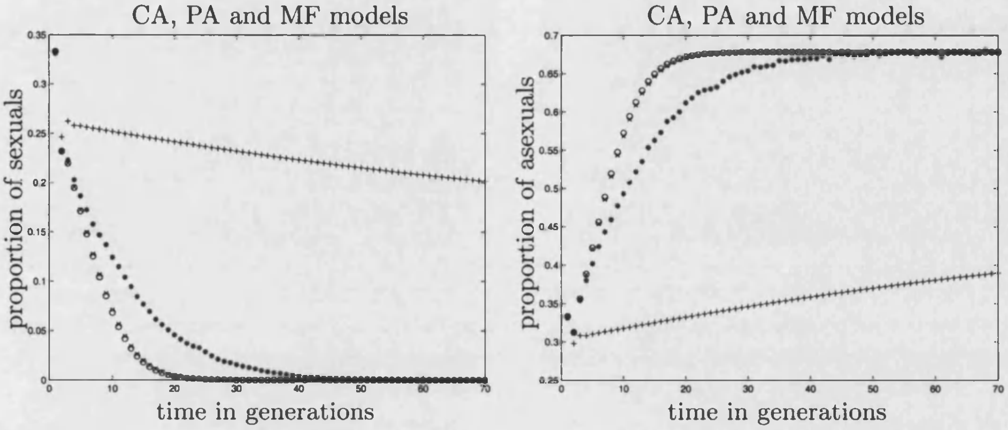


Figure 4.8: Results of a cellular automaton (*) simulation with $\sigma = 0.7$ and $\alpha = 0.3$. They are compared to those produced by the mean-field (+), local structure(o) and pair approximation (x). The figure on the left shows changes in the proportion of sexual individuals, while one on the right shows changes in the proportion of asexual individuals, along 70 generations. It is evident that the PA gives a better fit to the CA than does the MF. Notice also the contrasting behaviour of the CA and its mean field approximation, the latter exhibiting stable coexistence of sexual and asexual forms for these choice of parameters, while in the CA sexuals rapidly disappear.

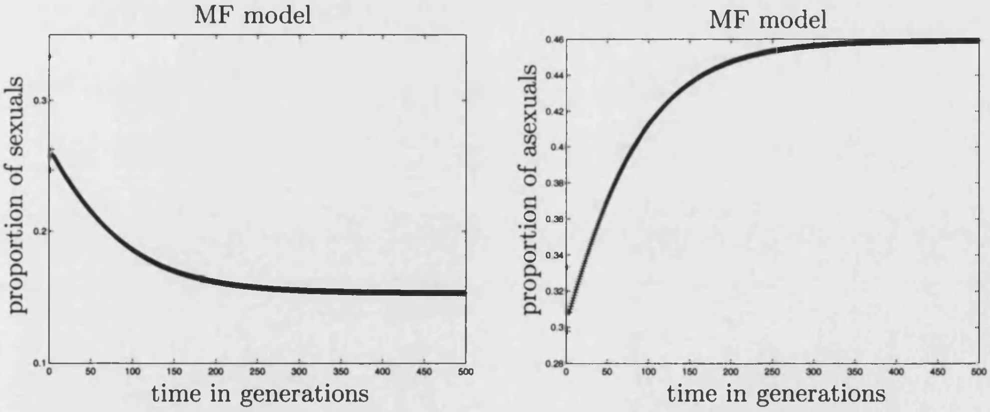


Figure 4.9: Results of a simulation of the mean-field model with $\sigma = 0.7$ and $\alpha = 0.3$. The behaviour of this model contrasts with that of the CA, as is made evident by this simulation spanning over 500 generations. Here, the MF clearly shows stable coexistence of sexual and asexual forms. The panel on the left shows the proportion of sexuals and the panel on the right shows the proportion of asexuals.

contrast between the cellular automaton and its mean field approximation. This may have especial relevance when modelling a population of flowering plants, where ecological interactions (fertilisation, pollen dispersal) between individuals occur at a scale much smaller than that of the whole population. From this point of view, a lattice structured model such as the cellular automaton is much more appropriate as a modelling tool.

Numerical simulations of the automaton enabled the building of large amounts of data for different values of parameters and initial conditions. These initial conditions were of various kinds: (1) a uniform distribution of empty, sexual and asexual cells; (2) a cluster of individuals of the same morph 'invading' a landscape where the other morph is uniformly distributed; (3) the same invading cluster in a landscape entirely dominated by the other morph with no empty spaces initially and (4) some individuals of one morph uniformly distributed over a landscape dominated by the other morph, with no empty spaces initially. These initial conditions also varied in the sexual/asexual ratio from as little as $0.04 : 100$ to $1 : 1$. Murrell *et al.* (2001) have highlighted the importance of initial conditions and this issue has been investigated with this new model.

Spatial clumping is a spontaneous result of a model with limited interactions (Harada and Iwasa, 1994, 1996), such as the CA. Individuals in a clump may have less empty cells to colonise in their immediate neighbourhoods. This assumption may be relaxed by allowing for long range dispersal of propagules. Locality may also affect fertilisation. Asexual individuals in a tight asexual clump may waste their pollen grains, whereas for sexuals clumping may ensure a supply of sexual pollen to produce sexual offspring. It could then be the case that male function in asexuals ceases to be advantageous in a clustering situation. Antonovics and Levin (1980) point out that organisms react to the effects of the number and proximity of their neighbours and not to the density of their populations. An individual-based model could help in the study of density-dependent factors on pollination and the coexistence of sexual and asexual forms.

This model is a good example of a system where the mean field approximation breaks down. While the cellular automaton does not allow for coexistence, the study of the parameter spaces for the corresponding mean field model shows non-negligible regions where stable coexistence is obtained, as well as regions of fixation of one morph. A possible explanation of the important qualitative differences in the behaviour of the mean field and CA models may reside in the fact that colonisation is only local in the CA. It is possible to show that this locality translates into a reduced effective colonisation rate, compared to that of the mean field model. Mean field analyses were, until recently, the most common tool to approach a CA. This and other models increasingly give the message that this tool has important limitations (Carrillo *et al.*, 2002.)

To this effect, analytic approximations that take into account spatial structure, such as a pair approximation, are useful to study to what extent restricted movement affects the dynamics of a population. Since colonisation only happens in empty nearest-neighbour cells, being in a cluster may be beneficial for flowering plants in terms of pollen supply, but disadvantageous in terms of colonisation as individuals stand in each other's way. By tracking local densities, a pair approximation can look into both of these issues. The quantities $q_{s/s}$ and $q_{a/s}$ give an idea of the effect on sexuals of the type and number of their neighbours, as they only reproduce through fertilisation. $q_{0/s}$, $q_{0/a}$ and $q_{0/0}$ help to understand how much individuals interfere in each other's colonisation processes. Other quantities of interest are $q_{s/s} + q_{a/s}$, $q_{a/a} + q_{s/a}$ and $1 - q_{0/0}/1 - p_0$, as they refer to mean crowding index for sexuals and asexuals and patchiness index of the whole landscape, respectively. Although the pair approximation did give a more accurate description of the CA, and in this respect is was a success, it still was a very complicated model in itself that relies heavily on lengthy computational work. This makes further insight into local issues difficult. To avoid this, it would be useful to consider a simplified version of the CA. Perhaps a one-dimensional CA. It would still allow for crowding and patchiness studies, while the size of the structures to be considered would be greatly reduced. Another possibility is to define rules that only require the examination of an 8-cell neighbourhood, rather than a 24-cell neighbourhood. This of course is work for the future, but what has been done so far has provided a new tool, namely a discrete-time pair approximation for complex ecological models.

Finally, it has also been seen that there are combinations of parameter values for which the fixation outcome will take thousands of generations to be realised. Although it is not possible to speak of polymorphic stable equilibria in the mathematical sense, coexistence, or presence of both sexual and asexual individuals, over thousands of years is obtained none the less. This may be called coexistence in a biological sense. One of the hypotheses put forward to explain the coexistence of sexual and asexual forms observed in the field is that the fixation outcome predicted by theory cannot be realised between glaciations, for it takes longer than an interglacial period (Britton and Mogie, 2001). These results of the cellular automaton are in accord with this hypothesis.

4.5 Future work

Another line for future research lies in the investigation of the effects of dispersal. Apart from the fact that the cellular automaton is a stochastic model while the corresponding patch-occupancy model is deterministic, the other main difference between the CA and the MF presented here is the restriction of ecological processes to nearest neighbours in the former. By modifying the size of the neighbourhood around a cell, and allowing dispersal of propagules (colonisation of empty patches) to take place in a larger neighbourhood, the CA becomes a useful tool to investigate long-range dispersal. Numerical experiments where colonisation is allowed within the 24 nearest neighbours of a given cell indicate that relaxed dispersal destabilises the characteristic exclusion results of the original cellular automaton. Indeed, with this new rule for dispersal, coexistence of sexual and asexual individuals is possible in a non-negligible region of the parameter space that is similar to the one observed in the mean field model (*cf.* figure 4.7, right panel). Figure 4.10 shows the results of a numerical simulation of the modified CA, where it is also possible to see a curious feature of the model with relaxed dispersal: there is evidence for cyclic behaviour. Tests to determine the existence of cycles, taken from time series analysis, applied to these data are shown in figure 4.11. They confirm the observation that the dynamics of the CA with larger dispersal range exhibit cycles, for certain parameter values. These results also mean coexistence in the mathematical sense. Unfortunately, the analytical limitations described before make it difficult to gain insight into what are the causes of this new behaviour. It would be desirable to understand if it is longer-range dispersal the only cause and if so, how it actually makes stable coexistence a possible result of the model when it was not observed in the original CA.

Spatial heterogeneity is perhaps the most logical progression in spatial modelling of ecological phenomena. If introduction of space was advocated for so as to make models more realistic, it is clear that space is not homogeneous. Further realism is added when spatial heterogeneity is taken into account. The CA can easily be modified to include a heterogeneous landscape. It suffices to declare some of the cells as of ‘poor quality’. Dispersing propagules that land in these cells do not germinate. They are lost to the count of future generations. Some numerical experiments with the CA included poor-quality patches as (i) uniformly distributed over the landscape; (ii) a cluster of 50 by 50 cells in the centre of the landscape; (iii) a 1-by-225-cell barrier which could represent obstacles such as a mountain range. These different initial conditions are shown in figure 4.12.

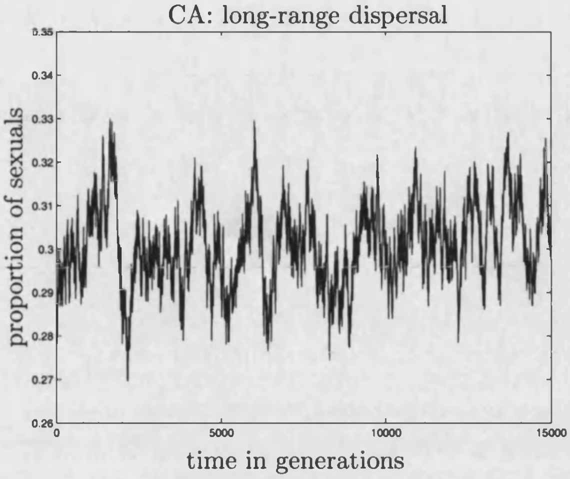


Figure 4.10: The simulation in the figure corresponds to the cellular automaton with modified dispersal rules. Under the new regime, propagules can settle in the empty patches of a 24-cell neighbourhood around their cell of origin. Changes in the proportion of sexual cells in time are shown here. It is clear that there is no tendency to exclusion of any of the types in the landscape. Moreover, there is evidence of cyclic behaviour. Although this simulation corresponds to $\sigma = 0.54$ and $\alpha = 0.26$, there are several other parameter values for which this behaviour is observed.

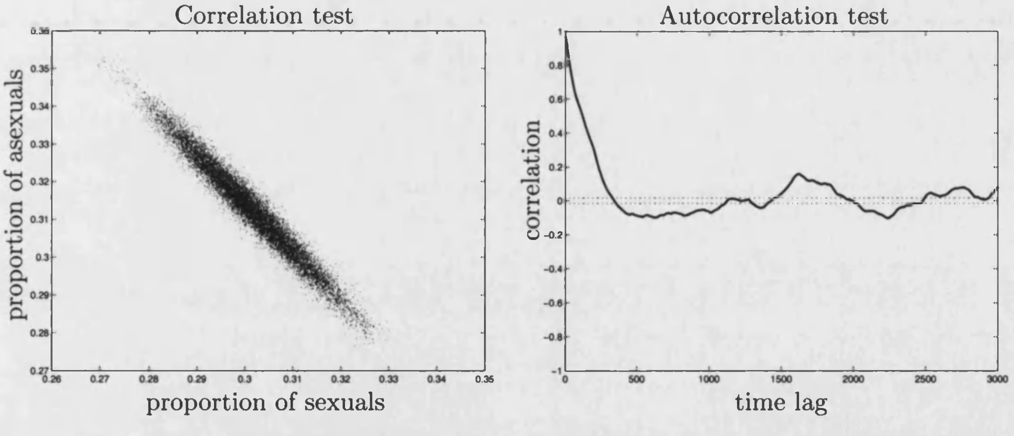


Figure 4.11: The figure shows the results of standard time series tests applied to the results of the CA with relaxed dispersal rules. The tests shown here were applied to the data generated by the modified CA using $\sigma = 0.54$ and $\alpha = 0.26$. Both correlation (left panel) and autocorrelation (right panel) are very strong. The band in the autocorrelation test is the region outside which there is statistical significance of the result. It can be seen that for most time lags, the results of the test are significant.

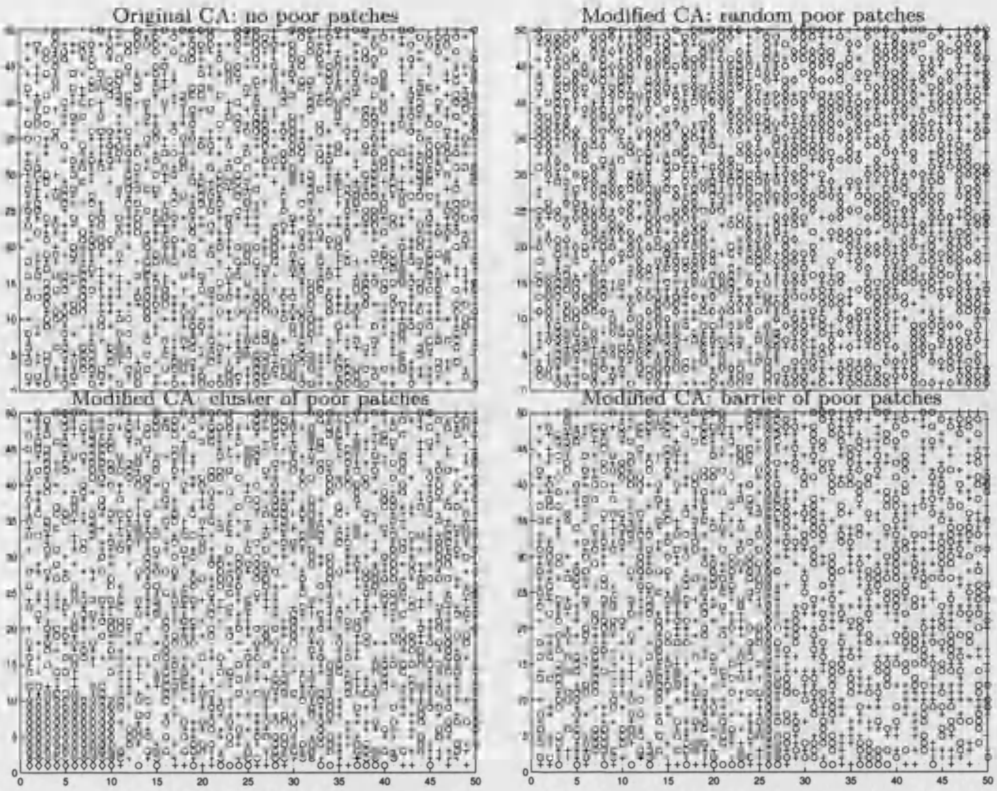


Figure 4.12: This figure shows initial conditions for the original CA and three modifications made in order to investigate the effects of spatial heterogeneity. In the original CA, the initial lansdcape consists of uniformly distributed sexual (o), asexual (+) and empty ( ) cells. The modified CA have landscapes where certain cells are of poor quality (marked by ◊) and thus not suitable for the population to settle there. These poor quality cells where introduced according to a uniform distribution, as a 50-by-50-cell cluster and as one column that represents a barrier in the landscape. As before, simulations were run using 225^2 gridsize, but only 50^2 is shown here for visual clarity.

Preliminary results indicate that the inclusion of these poor patches does not change the exclusion characteristic of the original CA shown in figure 4.13. Some simulations may run all 15,000 generations of the interglacial period without any type being completely excluded (marked by (*) in the space of results), but in all of them, one of the types is always very close to exclusion and would certainly disappear from the landscape if the simulation was allowed to run longer. The CA where poor patches are uniformly distributed in the landscape shows more of these extended-persistence episodes than any of the other modified cellular automata. Also, it shows that the region in the $\sigma - \alpha$ parameter space where sexuals dominate is reduced compared to the original CA. This can be seen in figure 4.14. The space of results for the other modified CA are shown in figures 4.15 and 4.16. More detailed local-structure studies need to be carried out to understand the observed differences.

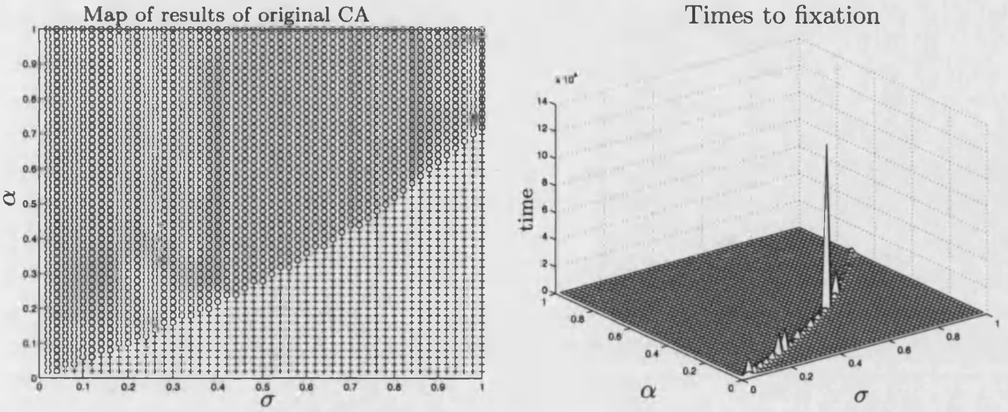


Figure 4.13: The figure shows results of simulations for the original CA, where the initial condition is a uniform distribution of sexual, asexual and empty cells. The panel on the left shows the results obtained over a $\sigma - \alpha$ parameter space. Fixation of sexuals is indicated by (o); fixation of asexuals by (+). There is no coexistence in the original CA. The panel on the right shows the times elapsed to witness the exclusion results.

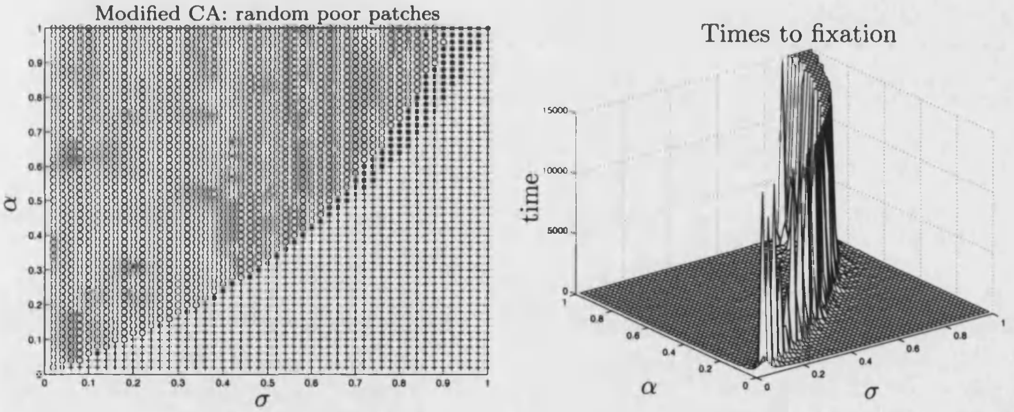
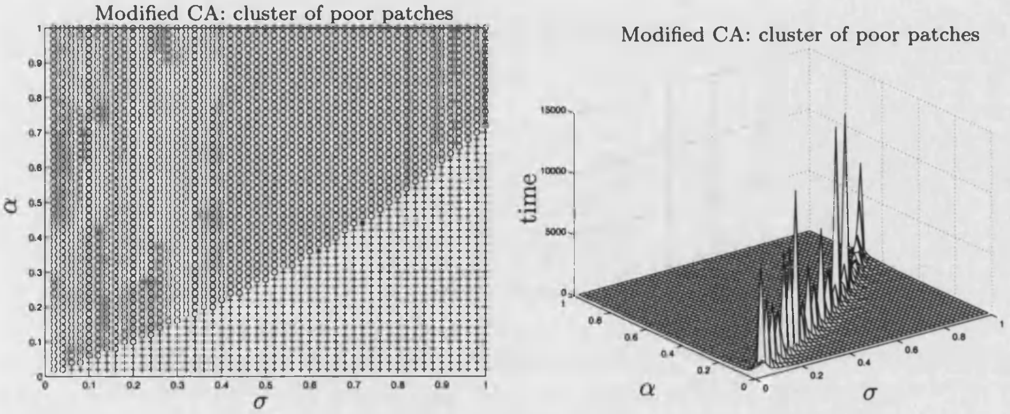
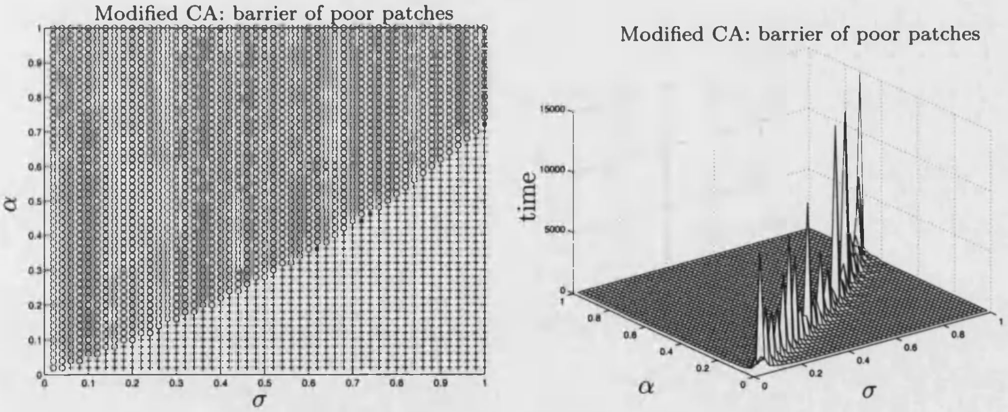


Figure 4.14: The figure shows results of simulations for the CA with initial condition that includes poor-quality patches uniformly distributed among sexual, asexual and empty cells. The panel on the left shows the results obtained over a $\sigma - \alpha$ parameter space. Fixation of sexuals is indicated by (o); fixation of asexuals by (+). There is no coexistence in this CA either, but those simulations that take longer than 15,000 generations to exclusion are marked by (*). The panel on the right shows the times elapsed to witness the results.


Modified CA: cluster of poor patches

Modified CA: cluster of poor patches

Figure 4.15: The figure shows results of simulations for the CA where the initial condition includes poor-quality patches in a cluster among a uniform distribution of sexual, asexual and empty cells. The panel on the left shows the results obtained over a $\sigma - \alpha$ parameter space. Fixation of sexuals is indicated by (o); fixation of asexuals by (+). There is no coexistence in this CA either, but those few simulations that take longer than 15,000 generations to exclusion are marked by (*). The panel on the right shows the times elapsed to witness the results.


Modified CA: barrier of poor patches

Modified CA: barrier of poor patches

Figure 4.16: The figure shows results of simulations for the CA where the initial condition includes poor-quality patches as a barrier in the middle of a uniform distribution of sexual, asexual and empty cells. The panel on the left shows the results obtained over a $\sigma - \alpha$ parameter space. Fixation of sexuals is indicated by (o); fixation of asexuals by (+). There is no coexistence in this CA either, but those few simulations that take longer than 15,000 generations to exclusion are marked by (*). The panel on the right shows the times elapsed to witness the results.

Appendix: Transient times in the CA model

This appendix shows figures of transient times of a simulation of the original CA model. For this simulation, mortality rates were given as $\sigma = 0.25$ and $\alpha = 0.3486$. This simulation was briefly shown in figure 4.2 as an example of an extended run where both sexual and asexual are present for thousands of generations before exclusion (of asexuals in this case) is clear. The figures that will be shown here are taken at equal time intervals through the simulation: (i) the initial landscape is given in figure 4.17; (ii) the landscape in the 3000th generation is given in 4.18; (iii) the 6000th generation is shown in figure 4.19; the 9000th generation is in figure 4.20; and generations 12000 and 15000 are given in figures 4.21 and 4.22, respectively. These landscapes show the complete grid of 225^2 cells. The clustering behaviour of sexual and asexuals is easily seen.

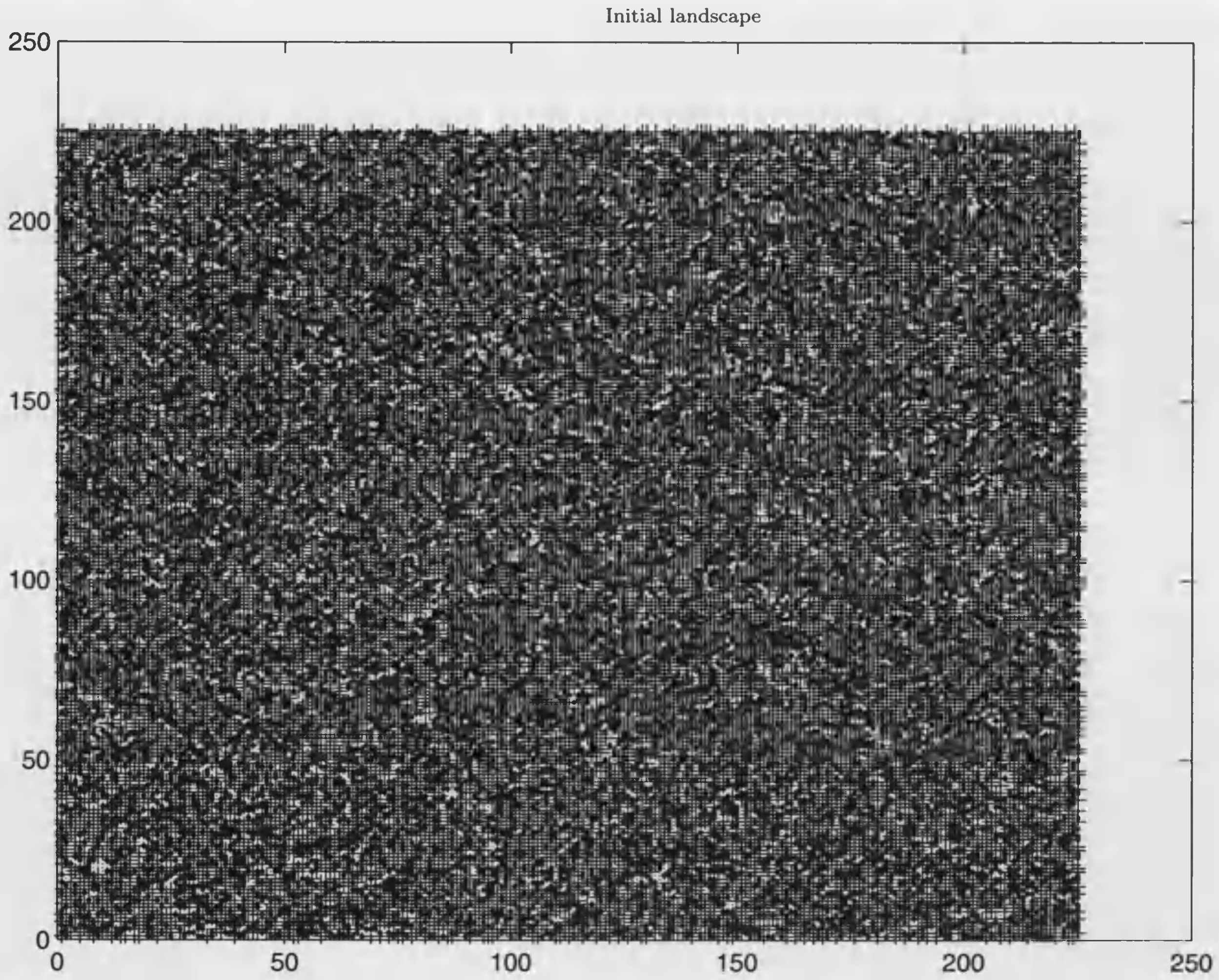


Figure 4.17: Initial landscape of a simulation of the CA model. The distribution of sexual (o), asexual (+) and empty cells ( ) is uniform.

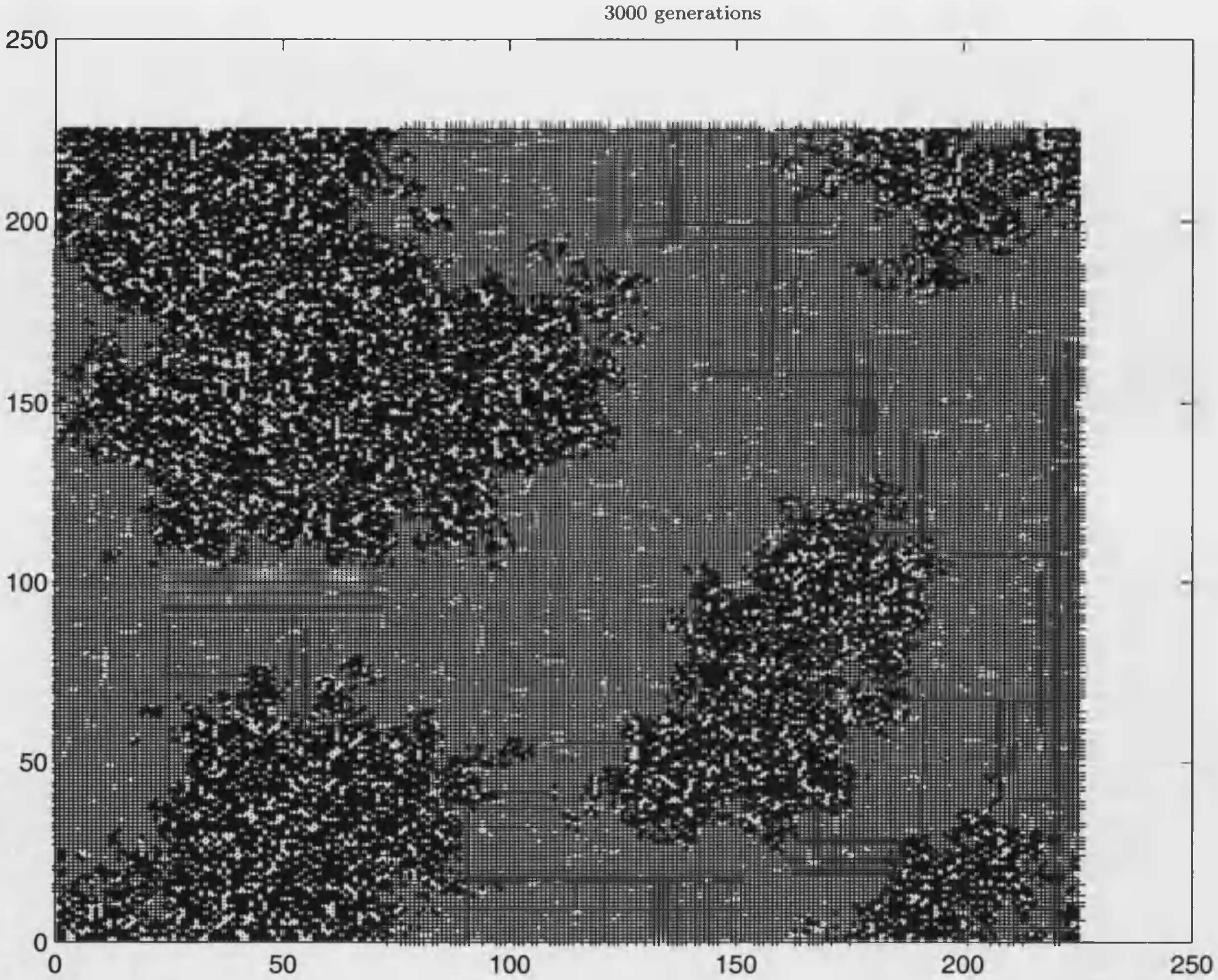


Figure 4.18: The landscape of a simulation of the CA model after 3000 generations have elapsed. Symbols: sexual (o), asexual (+) and empty cells ( ).

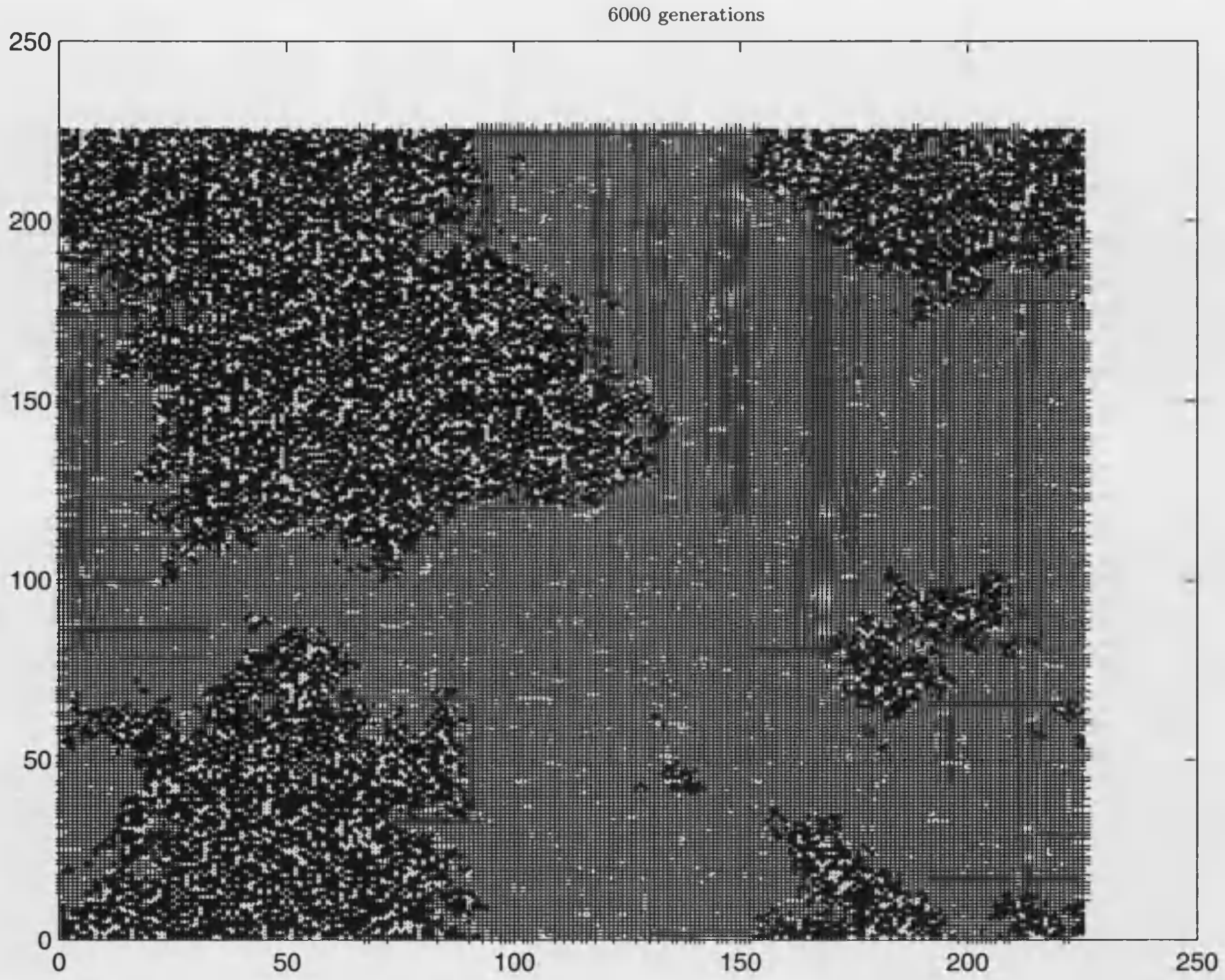
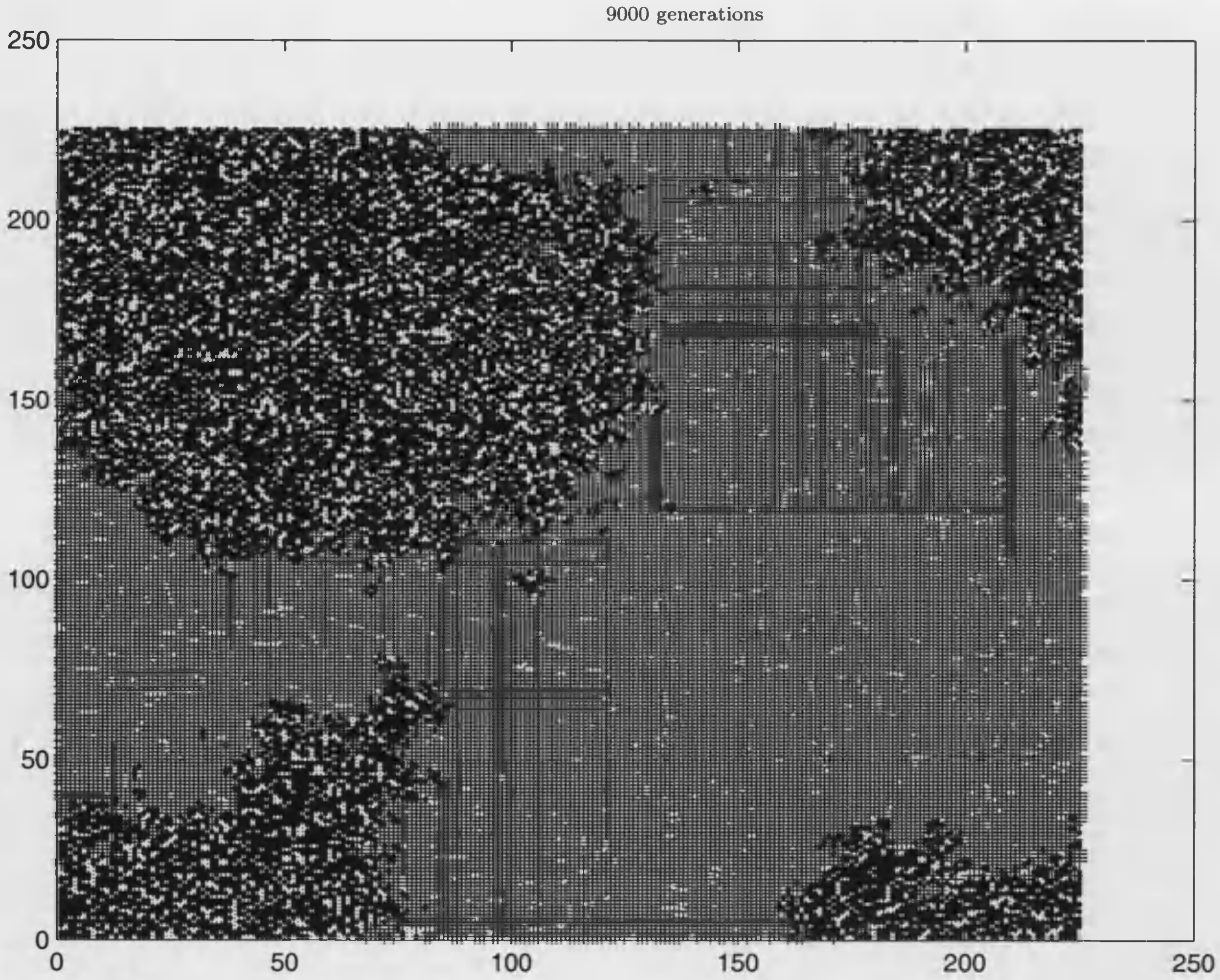


Figure 4.19: The landscape of a simulation of the CA model after 6000 generations have elapsed. Symbols: sexual (o), asexual (+) and empty cells ( ).



9000 generations

Figure 4.20: The landscape of a simulation of the CA model after 9000 generations have elapsed. Symbols: sexual (o), asexual (+) and empty cells ( ).

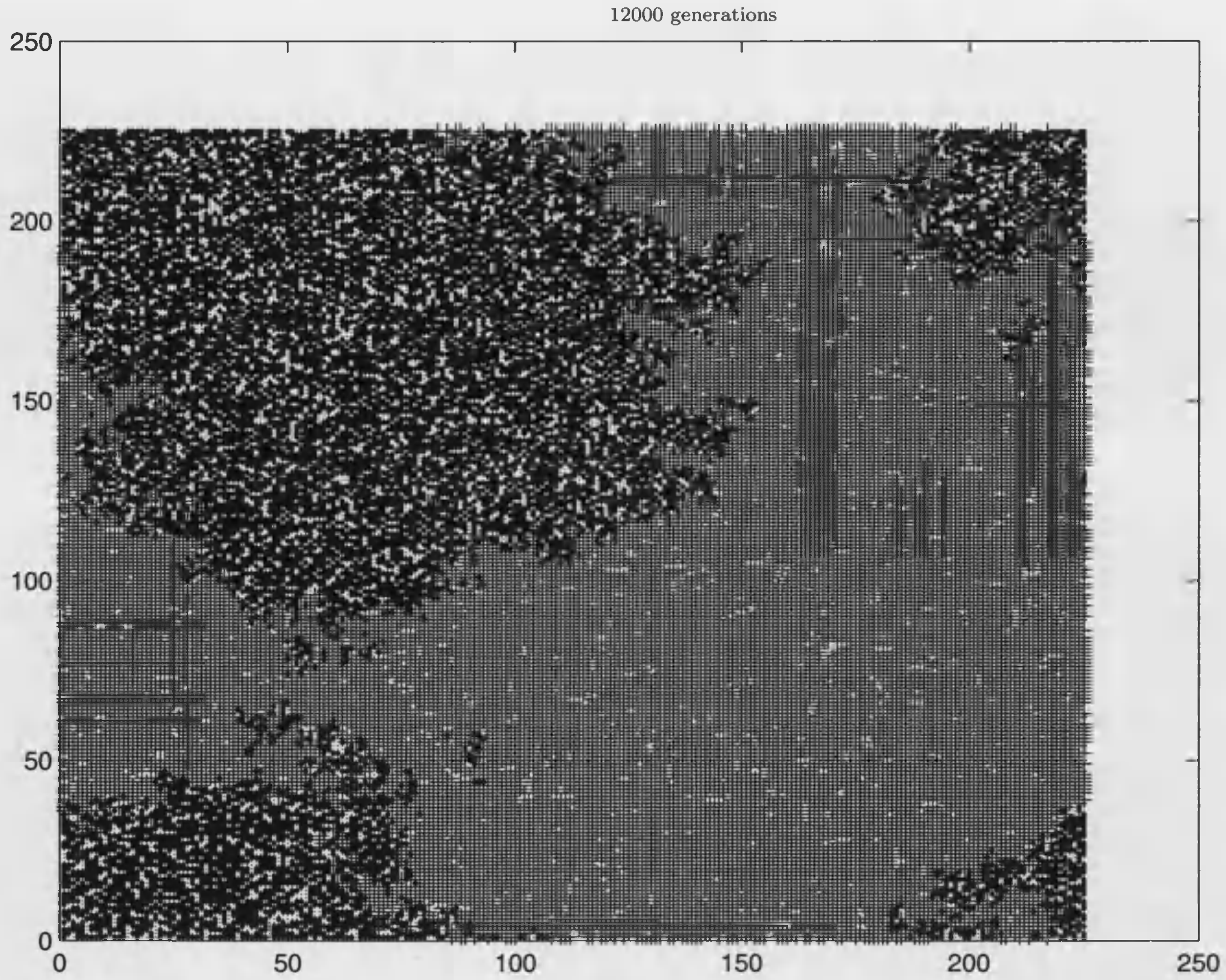


Figure 4.21: The landscape of a simulation of the CA model after 12000 generations have elapsed. Symbols: sexual (o), asexual (+) and empty cells ( ).

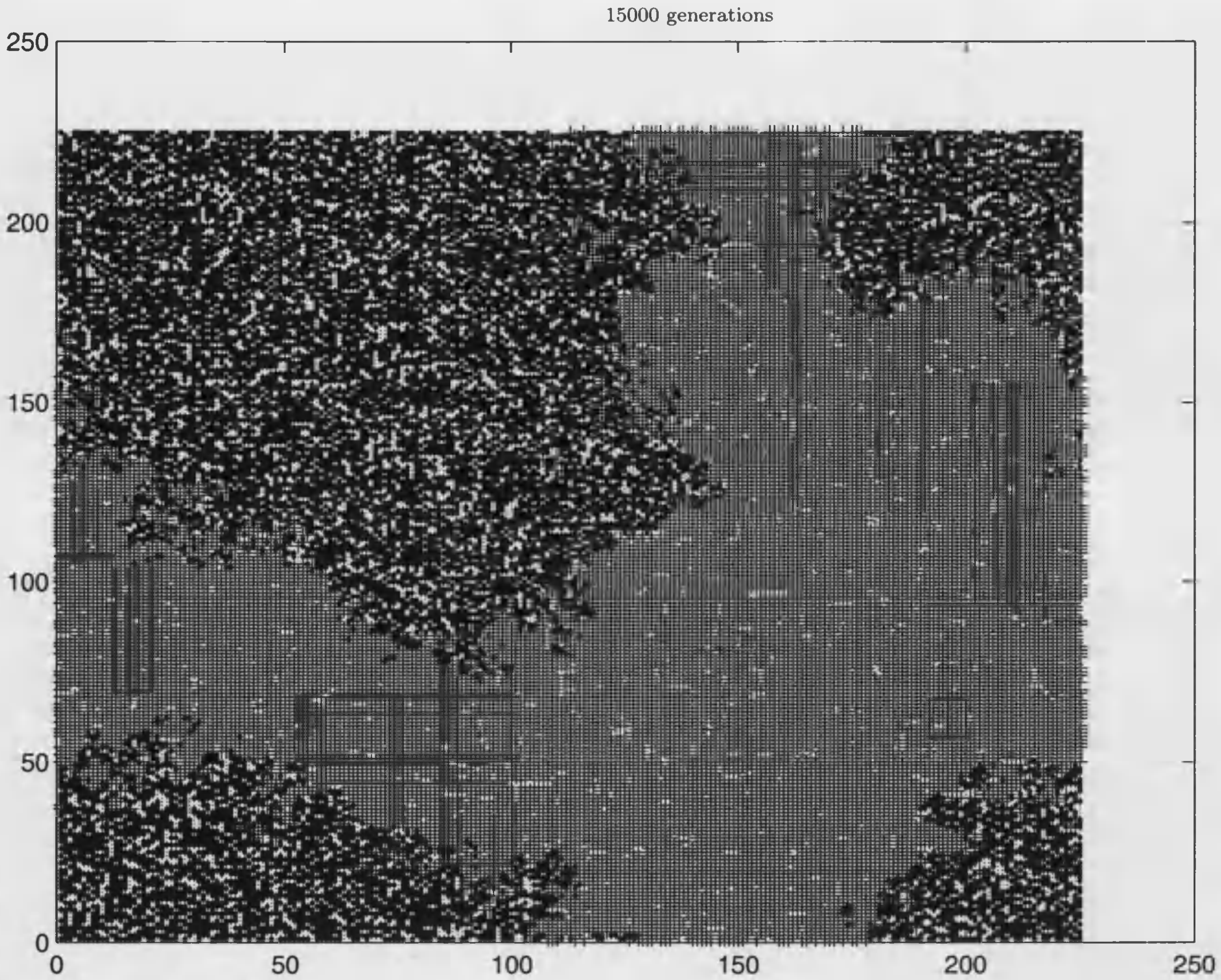


Figure 4.22: The final aspect of the landscape of a simulation of the CA model after 15000 generations have elapsed. These corresponds to the estimated length of an interglacial period, which is the time sexual and asexual populations are expected compete while expanding their ranges. Symbols: sexual (o), asexual (+) and empty cells ( ).

Chapter 5

The Reaction-Diffusion Approach to Sexuality *vs.* Asexuality: Dispersal of Propagules

Reaction-diffusion equations have been widely used to study the spread of invading organisms (Skellam, 1951; Roughgarden, 1986; Williamson, 1989; Hegenveld, 1989; Lewis and Kareiva, 1993; Shigesada *et al.*, 1980, 1986, 1987, 1997). Because biological invasions are constantly taking place, reshaping the distribution and abundance of species, they have been studied for both academic and practical purposes (Elton, 1958; Mooney and Drake 1987, 1989). The habitat of a species may become saturated by its presence or unsuitable due to disturbances, forcing some individuals to migrate. Invasion of a new suitable habitat occurs when some of these migrants colonise and persist in the new area, eventually expanding the range of their species (Shigesada and Kawasaki, 1997). Dispersal has always been observed as part of the life history of living creatures. Offspring usually have to establish their own survival space, even if in close vicinity to their parents. More recently, due to the influence of humans on most ecosystems, species travel around more often and faster, reaching and invading habitats that would have been completely out of their range otherwise. Also, the action of humans has dramatically increased the rate of deterioration and fragmentation of many habitats all over the world, forcing, in consequence, many species to migrate or even disappear. The bioengineering of new life forms that may escape controlled conditions and spread is another practical reason for the study of biological invasions.

More in connection to the subject of this thesis, reaction-diffusion equations have been used to study the spread of genes in a population (Fisher, 1937). This application plus other appearances of this kind of equations in physics (i.e. heat propagation, Brownian motion) from much earlier dates have yielded a vast literature on the subject (Kolmogorov *et al.*, 1937; Bramson, 1973; Kametaka, 1976; Fife, 1979). As a consequence, the mathematics of reacting and diffusing systems are sound and readily available, especially when it comes to applications in Biology (Britton, 1986; Murray, 1989; Shigesada and Kawasaki, 1997). The spread of a gene for asexuality arising in a sexual population has been studied through the reaction-diffusion approach by Britton and Mogie (2001). Borrowing from this theoretical framework, this work now proposes the reaction-diffusion approach to explain the coexistence of sexual and asexual forms. This, however, will not be a repetition of what Britton and Mogie have done, but an extension of their model aiming at incorporating long-range dispersal of propagules. Populations of flowering plants have been the chosen example of this thesis to illustrate the dynamics of a large group of organisms where sexual and asexual relatives coexist. As is usual with plants, they are sessile organisms. Very often, their progeny are equipped with ingenious mechanisms, such as parachutes or hooks, to be dispersed away from the parental entourage. Dispersal, in particular the range of dispersal, is another important spatial process in the ecology of populations and it will now be studied by means of a reaction-diffusion (RD) formalism.

5.1 Assumptions and the equations of the RD model

Modelling assumptions and notation remain as in the previous models. Just as a reminder, they are listed next:

1. Individuals are simultaneous hermaphrodites. Originally sexuals (s), their asexual (a) descendants have a modified female function that allows them to derive progeny from unfertilised eggs. N_s and N_a denote the number of sexual and asexual individuals in the population, respectively.

2. Asexuals have also retained a level of male function. Pollen produced by asexuals is divided into categories u, inviable, g_s, viable carrying gene s and g_a, viable carrying gene a. This model dispenses with the use of the parameter b for that pollen that leads to post-zygotic seed abortion. This is because the numerical simulations of the CA in the previous chapter showed that all pollen that leaves no descendants is equivalent, and thus only u is kept, comprising both inviable and polyploid pollen.

It should be noticed, moreover, that once an individual has acquired a copy of the mutant gene a, it becomes asexual. Thus, the following model will loosely refer to the spread of a gene for asexuality, while it really refers to those individuals carrying that gene.

As said before, the aim of this model is to reflect not only these aspects of the biology of the problem, but also the fact that the spread of a gene for asexuality is achieved by both short and long-distance dispersal. This is very clear in populations of flowering plants. Most extant asexual forms are descended from cosexual ancestors (Mogie, 1992). Although male and female function is found in the same individual, and sometimes even in the same flower, these plants have evolved mechanisms to avoid self fertilisation (Greenwood and Adams, 1987; Mogie, 1992). Pollen is often transported from one plant to near neighbours by insects, as seen in the previous chapter (Meagher, 1986; Bertin, 1988; Mogie and Stamp, 1995). That is, through male function, the dispersal of pollen and the genes it carries is very localised. On the other hand, there is the long-distance dispersal of propagules. Seeds, for example the parachute-equipped seeds of *Taraxacum*, tend to be wind-borne and thus may be dispersed over long distances. Measurements of the patterns of dispersal of seeds (Okubo and Levin, 1989; Fenner, 1992; Nathan and Mueller-Landau, 2000) show that most propagules settle in close proximity to the parents. This may provide a saturated environment in which only a few will be able to survive to maturity. These empirical studies of seed dispersal have also shown that a very important amount of propagules goes a long distance. The authors of these works argue that this kind of long-range dispersal is not negligible and has been under-estimated in traditional mathematical models than imply normal dispersal around the parent plant. No differentiation between sexuals and asexuals, in terms of dispersal, will be made. To sum up, in order for this model to include all the aspects discussed by means of a reaction-diffusion equation, it is necessary to have a term to account for the growth of the population, another term to account for short-distance dispersal and yet another to reflect long-distance dispersal.

The growth term is readily derived from the model of temporal dynamics. There, the numbers of sexual and asexual individuals from one generation to the next are given by the following equations:

$$N_s(t+1) = v_s \frac{k_f k_m (N_s(t))^2}{k_m N_s(t) + (1-u) k_m N_a(t)} + v_s \frac{k_f k_m N_s(t) g_s N_a(t)}{k_m N_s(t) + (1-u) k_m N_a(t)} \tag{5.1}$$

$$N_a(t+1) = v_s \frac{k_f N_s(t) g_a k_m N_a(t)}{k_m N_s(t) + (1-u) k_m N_a(t)} + v_a k_f N_a(t). \tag{5.2}$$

This time, however, the model will work with proportions rather than numbers of individuals. Let P_s and P_a denote the proportion of sexual and asexual individuals in the population at a certain time t and P'_s and P'_a denote these same proportions in the next generation. Using formulas (5.1) and (5.2), the following equations are obtained:

$$P'_s = \frac{N'_s}{N'_s + N'_a} = \frac{v_s N_s (N_s + g_s N_a)}{(v_s N_s + v_a N_a)(N_s + (1-u)N_a)} \tag{5.3}$$

and

$$P'_a = \frac{N'_a}{N'_s + N'_a} = \frac{N_a((v_s g_a + v_a)N_s + v_a(1-u)N_a)}{(v_s N_s + v_a N_a)(N_s + (1-u)N_a)}. \tag{5.4}$$

Introducing $\mu = \frac{v_s}{v_a}$ and using the fact that $\frac{N_s}{N_a} = \frac{P_s}{1-P_s} = \frac{1-P_a}{P_a}$, equations (5.3) and (5.4) can be rewritten as follows:

$$P'_s = \frac{\mu P_s (P_s + g_s(1-P_s))}{(\mu P_s + 1 - P_s)(P_s + (1-u)(1-P_s))}$$

and

$$P'_a = \frac{P_a((\mu g_a + 1)(1-P_a) + (1-u)P_a)}{(\mu(1-P_a) + P_a)(1-uP_a)}.$$

From the fact that $P_s + P_a = 1$, it is known that one of these proportions is fully determined by the other. From this point, P_s will be expressed in terms of P_a as $P_s = 1 - P_a$ and the model will work with one equation for the proportion of asexual individuals only. Thus, changes in P_a from one generation to the next are given by

$$P'_a - P_a = \frac{P_a((\mu g_a + 1)(1-P_a) + (1-u)P_a)}{(\mu(1-P_a) + P_a)(1-uP_a)} - P_a,$$

which may be transformed into

$$P'_a - P_a = \frac{(R_a - R_s)P_s P_a}{(R_s + 1)P_s + (R_a + 1)P_a},$$

where

$$R_s = (\mu g_s - 1)P_a + (\mu - 1)P_s \tag{5.5}$$

and

$$R_a = -uP_a + \mu g_a P_s \tag{5.6}$$

represent per capita reproductive success, for sexuals and asexuals respectively.

This will constitute the growth term of the model. Next, the diffusion term will be found.

As in Britton and Mogie (2001), it is assumed here that spatial variations in population levels can be described by defining population densities and that selection is weak. It will be assumed that the pairing of gametes takes place locally since pollen dispersal is often very localised and that the resulting offspring disperse randomly around their progenitors following an isotropic diffusion process given by

$$D\left(\frac{\partial^2 P_a}{\partial x^2}+\frac{\partial^2 P_a}{\partial y^2}\right),$$

where the diffusion coefficient D is a measure of how organisms disperse. Some of these propagules, however, may disperse over long distances, perhaps carried away by wind or water. It is important to include these adventurous propagules in the model. Typical modelling of dispersal by random diffusion only gives rise to normal patterns of dispersal. That is, it is assumed that most propagules are to be found near the focus of dispersal with the number rapidly decreasing to zero at more distant sites. But studies have shown that dispersal patterns tend to be leptokurtic rather than normal, with a non-negligible number of propagules reaching sites far away from the focus of dispersal (Crawford, 1984; Okubo and Levin, 1989). In chapter 1, a figure showing the main differences between normal and leptokurtic patterns of dispersal was given (*cf.* fig. 1.1). Mathematically, these dispersal patterns belong to different classes of functions: while the Gaussian distribution possesses a moment-generating function given by $M(s)=\mathrm{e}^{\sigma^2 s^2/2}$, leptokurtic patterns only have finite moments of all positive orders, but no moment-generating function. That is, if $k(z)$ describes a leptokurtic distribution, $\mu_n=\int_{-\infty}^{\infty} z^n k(z)dz$ is defined for $n\in\mathbb{N}$ only. Leptokurtic patterns could contribute to an increase in the speed of an invasion (Kot *et al.*, 1996). But in a diffusion-reaction model, the simplest way to include long-distance dispersal is by use of an advection term to represent a flow that carries away propagules (Shigesada *et al.*, 1997). An advection term has the form $\frac{\omega}{w_a}\frac{\partial P_a}{\partial x}$, where ω is the speed of the flow in direction x and w_a is a parameter that accounts for the differences, for example in weight, of sexual and asexual propagules.

Taking all the former factors into account, the complete reaction-diffusion model is given by

$$\frac{\partial P_a}{\partial t}=\frac{(R_a-R_s)P_sP_a}{(R_s+1)P_s+(R_a+1)P_a}+D\left(\frac{\partial^2 P_a}{\partial x^2}+\frac{\partial^2 P_a}{\partial y^2}\right)-\frac{\omega}{w_a}\frac{\partial P_a}{\partial x}. \tag{5.7}$$

A typical initial condition for the model in (5.7) has a shape close to a δ-function, for example

$$P_a(\overline{x},0) = \begin{cases} e^{\frac{1}{|\overline{x}|^2-1}}, & |\overline{x}| < 1, \\ 0, & |\overline{x}| \geq 1. \end{cases} \tag{5.8}$$

This kind of initial condition corresponds to a mutation localised in space.

5.2 Analysis of the model and results

The chief goal in this section is to find out if equation (5.7) has travelling wave solutions, so that the range and speed of the invasion it describes may be calculated. To study invasion by asexuals, it is necessary to find a solution of the form $P_a(\overline{x},t) = W(z)$, where $z = r_t - ct$, with $\overline{x} = (x,y)$, $c > 0$ and $r_t^2 = (x - \frac{\omega}{w_a}t)^2 + y^2$. This solution should satisfy the boundary conditions $W(-\infty) = 1$, and $W(\infty) = 0$. It is well known that travelling-wave type solutions to (5.7) play a fundamental role in the behaviour of solutions of initial value problems in the context of reaction-diffusion equations, in particular, of the initial value problem (5.7)-(5.8).

In this model, long-range dispersal of propagules is driven by a flow. The direction of the flow will be considered to be aligned with the x-axis. In general, if the flow moves in the direction of a vector $\overline{l} = (l_x, l_y)$ with speed ω, then we set $r_t = \sqrt{(x - \frac{\omega}{w_a}l_x t)^2 + (y - \frac{\omega}{w_a}l_y t)^2}$.

Notice that the function $W(r_t - ct)$ is a composition of the classical travelling wave solution of the reaction-diffusion equation without advection

$$\frac{\partial P_a}{\partial t} = \frac{(R_a - R_s)P_s P_a}{(R_s+1)P_s + (R_a+1)P_a} + D\left(\frac{\partial^2 P_a}{\partial x^2} + \frac{\partial^2 P_a}{\partial y^2}\right) \tag{5.9}$$

and the movement along the x-axis with speed $\frac{\omega}{w_a}$. This is why the study of equation (5.7) can be done along the lines of the classical travelling wave analysis of equation (5.9) with these results then being amended to take into account the constant-speed motion along the x-axis.

In view of this, substitution of the function $P_a(\overline{x},t) = W(r_t - ct)$ into equation (5.7) gives an ordinary differential equation of second order for the function $W(z)$ as follows:

$$-W'c = f(W) + DW'' + D\frac{W'}{r_t}, \tag{5.10}$$

where

$$f(W) := \frac{(R_a(W) - R_s(W))(1-W)W}{(R_s(W)+1)(1-W) + (R_a(W)+1)W} \tag{5.11}$$

with (*cf.* (5.5) and (5.6))

$$R_s(W) = (\mu g_s - 1)W + (\mu - 1)(1-W) \tag{5.12}$$

and

$$R_a(W) = -uW + \mu g_a(1-W). \tag{5.13}$$

The equation (5.10) can be approximated, for sufficiently large r_t (Lewis and Kareiva, 1993), by the following equation

$$-W'c = f(W) + DW''. \tag{5.14}$$

It is a standard observation that this second-order ordinary differential equation is equivalent to a system of ordinary differential equations of first order:

$$W' = V, \tag{5.15}$$

$$V' = \frac{-f(W)}{D} - \frac{c}{D}V. \tag{5.16}$$

The steady states of this system are found when both $W' = 0$ and $V' = 0$. That is, when $V = 0$ and $V = \frac{-f(W)}{c}$, so that the steady states of the system (5.15)–(5.16) are in fact points $(0, W_i)$, where W_i are zeros of the function f. It is easy to see, from (5.11), that $f(W) = 0$ if $W = 0$, $W = 1$ or $R_s(W) = R_a(W)$. Let W^* be defined as the value of W where $R_s(W) = R_a(W)$. In view of the formulas (5.12) and (5.13), this value is given by the following formula

$$W^* = \frac{\mu(1-g_a) - 1}{u(\mu - 1)}.$$

It is well known that, qualitatively, the behaviour of the dynamical system (5.15)–(5.16) depends on where the point $W = W^*$ is situated with respect to the other two zeros of the function f, that is, $W = 0$ and $W = 1$. This sets the following conditions for the parameter μ :

$$\text{(i) } W^* > 0 \text{ if and only if } \mu > \frac{1}{1-g_a}$$

and

(ii) $W^* < 1$ if and only if $\mu < \dfrac{1-u}{g_s}$.

The values of the parameter μ shall thus act as a guide to mark the different cases that we have to study in order to analyse the model.

Case 1. $\mu < \frac{1}{1-g_a}$. Under this condition, the dynamical system (5.15)–(5.16) exhibits only two steady states of interest: $(0,0)$ and $(1,0)$. Moreover, $f'(0) > 0$ and $f'(1) < 0$, so that $f(W) > 0$ in $(0,1)$. By means of a standard local stability analysis, it is easy to see that $(0,0)$ is a stable node when $c > 2\sqrt{Df'(0)}$ and that $(1,0)$ is a saddle point. It is known that in the phase plane there are two trajectories emanating from $(1,0)$. It can be shown (Fife, 1979) that for any $c > 2\sqrt{Df'(0)}$ one of those trajectories connects to $(0,0)$. This trajectory corresponds to a wave front solution of (5.14) with $W(-\infty) = 1$ and $W(\infty) = 0$.

Furthermore, the solution to the initial value problem (5.9)–(5.8) converges uniformly in x to the function $W(r_0 - c^*t - \psi(t))$, where $c^* = 2\sqrt{Df'(0)}$ and $\psi'(t) \to 0$ as $t \to \infty$ (Fife, 1979 and other references therein). Therefore, it is expected to observe invasion by asexuals with speed close to c^*. Note that in terms of the parameters of the model $c^* = 2\sqrt{D\mu^{-1}(1-\mu+\mu g_a)}$. The speed of the front of the solution $P_a(\bar{x},t)$ to the initial value problem (5.7)–(5.8) is thus given by the expression $c^* + \frac{\omega}{w_a} = 2\sqrt{D\mu^{-1}(1-\mu+\mu g_a)} + \frac{\omega}{w_a}$. However, a bell-shaped initial condition has been set, which then spreads isotropically. This means that the invading front is followed by a rear front which is also affected by the constant speed of movement along the x-axis. This rear front will 'expand' in its own right only if $\frac{\omega}{w_a} - c^* < 0$, that is, the ratio of the speed of the flow and the weight factor is not larger than the classical invasion speed found in the study of (5.9). If this condition is not fulfilled, asexuals sweep through the landscape rather than invade as the rear front recedes. See figure 5.1.

Case 2. $\frac{1}{1-g_a} < \mu < \frac{1-u}{g_s}$. As seen before, when μ lies in this interval, the function $f(W)$ defined in (5.11) has three zeros: $W = 0$, $W = 1$ and W^*. These correspond in turn with steady states of the system (5.15)–(5.16). Through a local stability analysis it is straight forward to realise that both $(0,0)$ and $(1,0)$ are saddle points since $f'(0) < 0$ and $f'(1) < 0$. The point $(W^*, 0)$ may be either a stable node or a stable focus, depending on the sign of the value $(\frac{c}{D})^2 - 4\frac{f'(W^*)}{D}$. An analysis of the vector field generated by the dynamical system (5.15)–(5.16) over the five regions in which the two zeroclines $V = 0$ and $V = \frac{-f(W)}{c}$ divide the phase plane $W - V$ allows some hope that among the trajectories emanating from $(1,0)$ one of them may come into $(0,0)$ and give the travelling wave front looked for. However, the steady state in the middle is stable and may attract

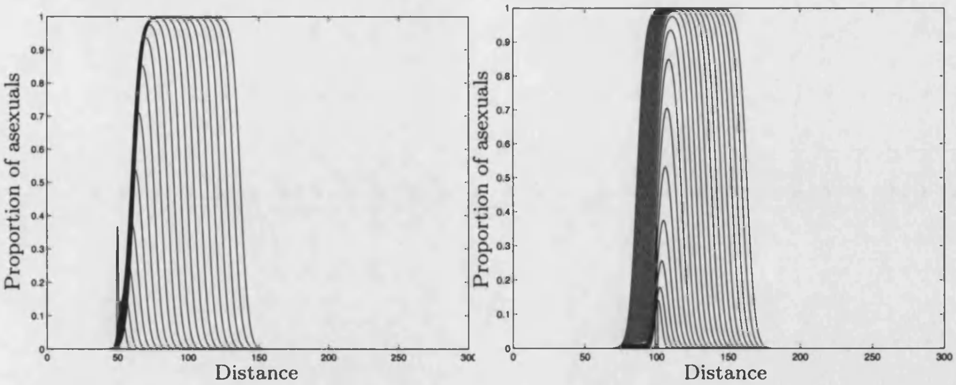


Figure 5.1: The figure shows a simulation of the RD model with an advection term for long-distance dispersal. It can be seen that the wave of invasion is the same, with its velocity modified precisely by the value of the speed of the flow in the advection term. The rear front of the invasion recedes when $\frac{\omega}{w_a} - c^* > 0$ (left) but advances otherwise (right). In this simulation $\mu = 1$, $g_s = g_a = 0.25$, $w_a = 1$ and $\omega = 1$ (left panel) and $\omega = 0.5$ (right panel). The time interval between consecutive profiles in the figure is 2.5 time units.

trajectories emanating from $(1, 0)$. It can be shown (see, for instance, Fife, 1979) that there exists a unique $c^* \in (-\infty, \infty)$ such that for $c = c^*$, equation (5.9) has a travelling wave solution $W(r_0 - ct)$ with $W(-\infty) = 1$ and $W(\infty) = 0$. Moreover, such a travelling wave moves in the outward direction, *i.e.* $c^* > 0$ if and only if

$$\int_0^1 f(W)dW > 0. \tag{5.17}$$

Furthermore, if $P_a(\overline{x}, 0) > W^* + \delta$ over a sufficiently large spatial range $L = L(\delta)$, where $\delta > 0$, then the solution of the initial value problem (5.9)–(5.8) converges uniformly in x to a travelling wave solution $W(r_0 - c^*t - z_0)$ when $t \longrightarrow \infty$, where z_0 is a constant (see Fife, 1979). Therefore the solution of the initial value problem (5.7)–(5.8) converges to a travelling wave $W(r_t - c^*t - z_0)$.

In biological terms, this mathematical result can be read as conditioned invasion. If the initial proportion of asexuals is above a threshold value given precisely by W^* and a certain critical viability coefficient μ_c determined by (5.17) is not surpassed, then asexuals will invade. Otherwise, the invasion dies out and sexuals may invade, also in a conditioned way. Figure 5.2 shows an example where conditioned invasion of asexuals is obtained. Finding an initial condition that satisfied the required inequalities was a non-trivial numerical task and the example is somewhat crude, but it illustrates the case of conditioned invasion.

Case 3. $\mu > \frac{1-u}{g_s}$. In this case, there is no travelling wave solution of equation (5.14) with the specified boundary conditions. In the phase plane portrait of the dynamical system (5.15)–(5.16), it is impossible to find a trajectory $V(W) < 0$

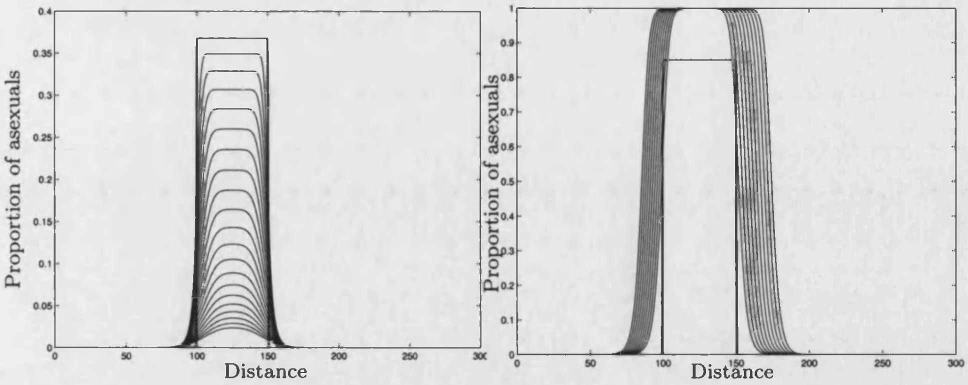


Figure 5.2: The figure shows conditioned invasion of asexuals. When the initial population has not surpassed a critical density, the invasion fails, as shown in the left panel. In the right panel, due to a sufficiently robust initial density of asexuals over a sufficiently large spatial range, as described in case 2 of the analysis, the invasion is successful. In this simulation, $\mu = 1.5$, $g_s = g_a = 0.25$, $u = 0.5$, $\omega = 0.01$ and $w_a = 1$. For the unsuccessful invasion, the time interval between consecutive profiles is 2.5 time units. Since the successful invasion is relatively slow, the time between consecutive profiles is set at 50 time units.

from $(1, 0)$ to $(0, 0)$ and any invasion of asexuals will die out. There are, however, trajectories $V(W) > 0$ from $(0, 0)$ to $(1, 0)$ that describe invasion by sexuals. The numerical simulation in figure 5.3 shows a failed invasion of asexuals.

5.3 Discussion

One of the main assumptions of the model is that sexually and asexually produced propagules do not have the same viability. This is reflected in the parameters v_s and v_a and their quotient μ. The worst scenario for sexuals is set when there are no costs to asexuality. That is, when all asexual male gametes are fully functional, which in terms of the parameters of the model is given by $u = 0$, $g_s = g_a = \frac{1}{2}$. In this case, asexuality will go to fixation for any initial condition as long as $\mu < 2$. Similarly, asexuals will not invade, regardless of the initial condition, if $\mu > 2$. This case recovers the typical models of sex where there is a two-fold cost associated with sexuality. It is, however, assumed that there are certain costs associated with a shift to asexual reproduction. Such costs have been reflected in other models as a reduction in the male output of asexuals (Joshi and Moody, 1995, 1998). While there is no evidence that this reduction is an intrinsic feature of asexuality, there is ample evidence to support our assumption that asexually produced male gametes may be of poorer quality when compared to sexually produced ones, thus the differences in the viabilities of the corresponding

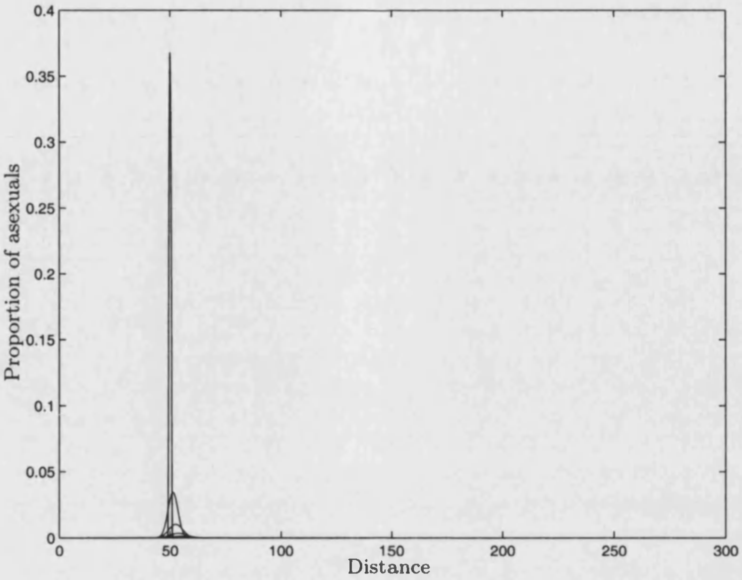


Figure 5.3: The figure shows how invasion by asexuals fails whenever $\mu > \frac{1-u}{g_s}$, even if there is long-distance dispersal. For this simulation, parameter values are: $\mu = 2.5$, $g_s = g_s = 0.25$, $u = 0.5$, $\omega = 0.5$, $w_a = 1$. The time between consecutive profiles is 2.5 time units.

offspring. In this model, invasion of asexuality is contemplated in case 1, where an invasion is guaranteed for any initial condition when $\mu < \frac{1}{1-g_a}$. When the values of μ are in the range $(\frac{1}{1-g_a}, \frac{1-u}{g_s})$, there is also the possibility of an invasion, but it is subject to some conditions: (i) the initial proportion of asexuals has to exceed W^* over a sufficiently large spatial range L and (ii) a critical value μ_c should not be exceeded as far as viabilities are concerned. Finally, asexuals cannot invade a sexual population, for any initial proportion, when $\mu > \frac{1-u}{g_s}$.

Another key feature of the model is the inclusion of long-distance dispersal by means of an advection term that represents dispersal of propagules carried away by wind or other kind of flow. This term was included to study the role played by these long-distance dispersers since it has been suggested that the speed of an invasion would be increased when dispersal patterns are leptokurtic (Kot *et al.*, 1996) as compared to normal. In comparison to models where there is no advection term and dispersal of propagules follows a normal distribution (Britton and Mogie, 2001), it can be seen, from numerical simulations, that the speed of the flow does give a boost to the speed of the front (see figure 5.4). Namely, when a frontal wave can be found, it propagates with speed $c^* + \frac{\omega}{w_a} > c^*$.

However, this contribution is not enough to change the qualitative behaviour of the results: essentially, two values of μ, μ_1 and μ_2, can be found for models with normal dispersal such that below μ_1 invasion of asexuals occurs for any

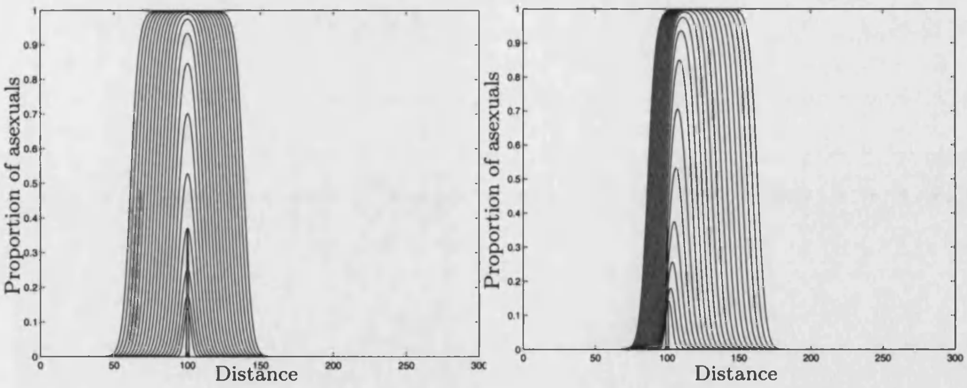


Figure 5.4: Invasion is aided by long-distance dispersal in the simulation in the figure. The speed of the flow does give a boost to the speed of invasion (right panel) as compared to the pattern of invasion observed for a formulation of the model without the advection term of long-range dispersal (left panel). Parameter values are: $\mu = 1$, $g_s = g_a = 0.25$, $u = 0.5$, $w_a = 1$, $\omega = 0$ (left) and $\omega = 0.5$ (right). Time interval between profiles: 2.5 time units.

initial condition, between μ_1 and μ_2 there is the possibility of conditioned invasion and above μ_2 no invasion can occur (see figure 5.5). In short, the way in which long-distance dispersal was introduced in the model has yielded increased speeds of invasion, but not substantial ones. The advection term, on the other hand, also accounts for the differences between sexual and asexual propagules as dispersers. The parameter w_a has been included to reflect such differences. Numerical simulations provide the opportunity to study the extent to which the model is sensitive to changes in w_a, which is of importance for the study of sexuality *vs* asexuality (see figure 5.6). In some flowering plant species, where both sexual and asexual types are observed, such as *Taraxacum*, asexual propagules tend to be heavier than sexual propagules (Mogie, 1992; de Kovel and de Jong, 1999) which could make them worse dispersal agents.

Finally, the model also allows us to have a first insight into the geographic distribution of sex. Once again, dandelions are a good example of a species that presents geographic parthenogenesis. In Europe, for example, sexual forms are common in France and Slovenia, with more than 50% presence in those sites. This percentage diminishes over a small range where both sexual and asexual forms coexist, until it practically vanishes towards the north. Few if any of the populations of *Taraxacum* in Great Britain are sexual (Dudman and Richards, 1997) while in continental Europe sexual forms reach their northernmost limit in the Netherlands (van Baarlen *et al.*, 2000). Many hypotheses have been put forward to explain this spatial differentiation: tangled bank and Red Queen hypotheses suggest that sexuals are better suited to rich, packed and fluctuating environments

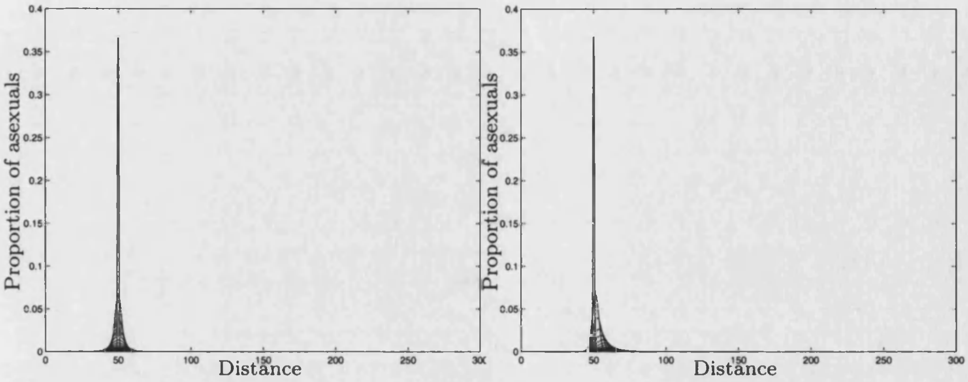


Figure 5.5: The figure shows how long-distance dispersal modelled by an advection term does not affect the qualitative behaviour observed in models with normal diffusion only (Britton and Mogie, 2001). In this graph, invasion by asexuals fails even when aided by long-distance dispersal (right panel), as it would in the model without the advection term (left panel). The ranges reached, however, are larger than those reached by normal diffusion alone. Parameters are set as follows: $\mu = 1.5$, $g_s = g_a = 0.25$, $u = 0.5$, $w_a = 1$, $\omega = 0$ (left) and $\omega = 0.5$ (right). Time between profiles: 2.5 time units.

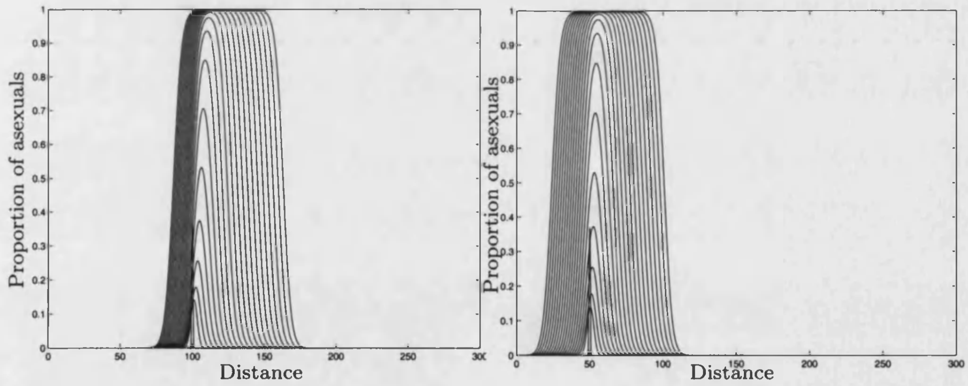


Figure 5.6: The figure shows that the model is sensitive to changes in the parameter w_a, which reflects differences between propagules. For lighter propagules (left panel), there is a slight increase in the range attained by the population. Parameter values are: $\mu = 1$, $g_s = g_a = 0.25$, $u = 0.5$, $\omega = 0.5$, $w_a = 1$ (left) and $w_a = 2$ (right). The time interval between consecutive profiles is 2.5 time units.

whereas the superior colonising ability of asexuals would allow them to establish in more extreme environments where the pressure from pests, pathogens or competitors is low (Gishelin, 1974; Vrijenhoek, 1984; Weeks, 1993). In particular, this would allow asexuals to move into areas that were under ice during the last Ice Age (Bierzychudek, 1985, 1987) thus explaining their European ranges. Numerical simulations of the model suggest that the front of an invasion advances as much as 1.65 m/year (for $\mu = 1.5$, $g_s = g_a = 0.25$, $\omega = 1$ and $w_a = 1$). This is a very slow invasion. Even considering 15,000 years as the duration of an interglacial period, the range would only expand 30 km, which certainly does not correspond to observed incursions of asexuals into virgin territory (Northern Europe). Thus, without successful long-distance dispersal, distributions would hardly change, even between glaciations. This is similar to results found by Skellam (1951). The way in which the invasion of a sexual population by asexuals was modelled suggests that it takes long time to be realised and may explain why sexual and asexual forms are seen to be coexisting. It is thus inferred that an invasion cannot be completed during an interglacial period. But, also, resulting speeds are so low that one could not witness any changes in the first place. Therefore, new ways of including long-distance dispersal should be investigated.

5.4 Future work

The reaction-diffusion model proposed in this chapter can be modified in order to investigate long-range dispersal in an alternative way. The Gaussian dispersal mechanism implicit in the Laplacian operator in (5.9) very appropriately describes neighbourhood diffusion experienced by propagules which disperse in a random-walk fashion around the parent plant. Apart from this founder or primary population, long-range dispersal can be added by using secondary nuclei of spread founded by propagules that reached further than the mean of their siblings. The delta-like initial condition of the model in (5.9) can be modified so that there are several centres of spread or, alternatively, these secondary centres are sporadically generated by the established populations. For simplicity, all these loci initiate with exactly the same density. However, a more realistic modification would be to have a primary locus of spread with a given population density and secondary loci of spread away from the primary one with lesser population densities as their distance from the primary population increases. This would reflect the fact that as the population spreads, only a few, but significant, individuals disperse over longer ranges and may initiate a secondary population. Simulations

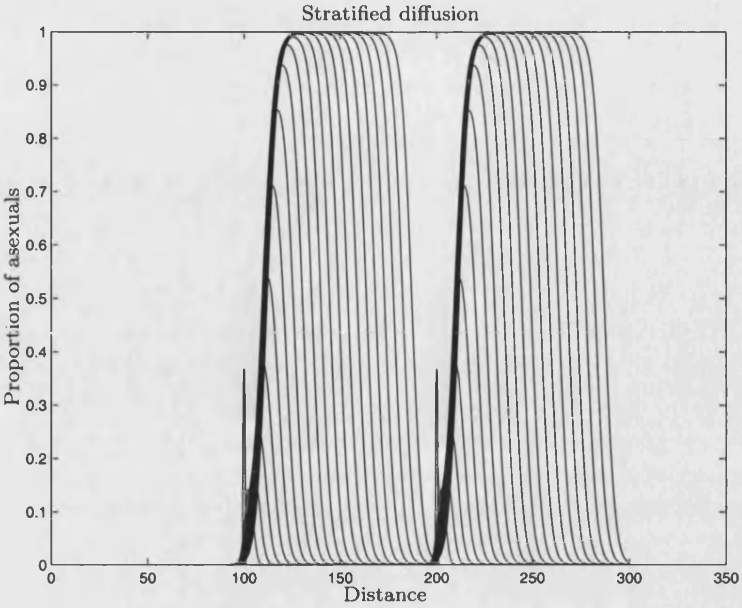


Figure 5.7: The figure shows the spread of two subpopulations up to the moment they collide. Eventually, coalescing subpopulations move as one front. Parameter values used for this simulation are: $\mu = 1$, $g_s = g_a = 0.25$, $\omega = 1$ and $w_a = 1$. As in other simulations, the time interval between consecutive profiles is 2.5 time units. The observed shift to the right is due to the advection term in the model.

of the modified model follow the evolution of all subpopulations in time. In particular, it is important to understand if these subpopulations will spread until they collide and become one larger population and how this combined diffusion, termed stratified diffusion by Hegenveld (1989), affects the rate of spread of the population. Figure 5.7 shows a numerical simulation of the model in this chapter, (5.7) for an initial condition with two centres of spread. A thorough treatment of stratified diffusion for Fisher's model is offered by Shigesada and Kawasaki (1997); they also discuss scattered and coalescing stratified diffusion. For more complicated models, however, most of the analysis has to rely on numerical work.

In spite of its limitations, this model could also be used to study the effects of spatial heterogeneity. Using precisely this model would have the advantage that, since the results of the original model are well understood, any changes observed in the results would have to be attributed to the heterogeneous landscape. A first way to introduce a heterogeneous landscape is to declare some intervals of the one-dimensional habitat as 'poor-quality terrain'. The population has a different diffusion coefficient in such places. As a start, these poor areas have been introduced uniformly along the habitat. The length of these intervals is one of the factors that can be modified. This length can be given different measures,

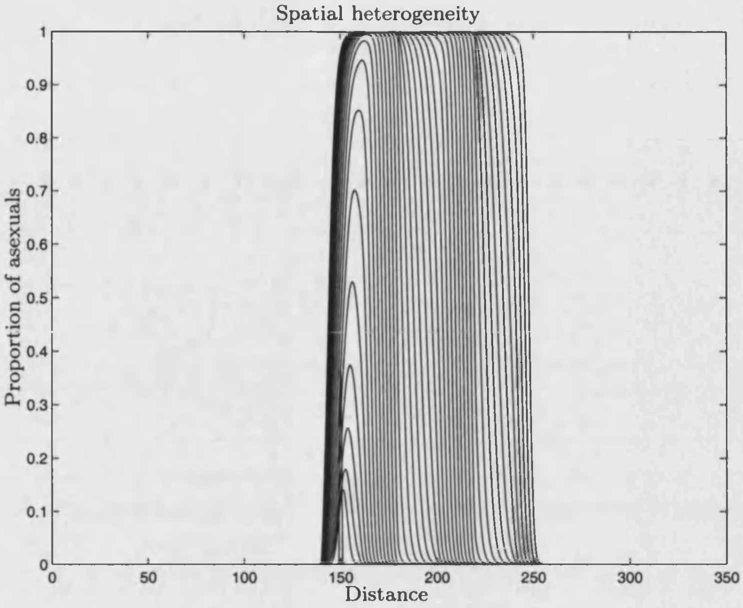


Figure 5.8: The figure shows a population spreading over a heterogeneous landscape. Every 20 units of distance, the terrain changes from good to poor quality and consequently affects the diffusion coefficient. This decreases from a normal value of 1 to 0.5 in poor terrain.

according to what is relevant for a given system. Once more, this brings the topic of this research close to the discussion about the effective ecological and genetic neighbourhoods. For simplicity, all intervals are equal in length, but this is not necessarily so in a real system.

The results of numerical simulations show that spread will be faster in those regions with higher diffusion coefficient. Also, the profiles obtained "undulate" due to the difference in the diffusion coefficients. These undulatory effect is more notorious when both the diffusion coefficient and the intrinsic growth rate of a population vary due to spatial heterogeneity. Shigesada and Kawasaki (1997) have shown this for the Fisher model; the effect is know as a periodic travelling wave. Here, in figure 5.8, results of a simulation of the RD model with a heterogeneous landscape are given. The population has a delta-like initial condition and spreads over a landscape that changes its quality every 20 units of distance. In poor quality terrain, the diffusion coefficient is lower than in good terrain. The intrinsic growth rate has not been modified. Thus, it is difficult to perceive the undulating profiles.

Chapter 6

Dispersal Revisited in a System of Two Integro-difference Equations with Exponentially-Bounded Kernels

This chapter investigates the role of long-range dispersal in the coexistence of sexual and asexual relatives in a population of hermaphrodite flowering plants. In these populations, growth and reproduction occur during a sedentary stage that is then followed by wind dispersal of propagules. These two stages are clearly distinguishable and show strong seasonality. A modelling approach that accurately describes these dynamics of mixed populations is a system of two non-linear integro-difference equations. This kind of equation can in principle accommodate dispersal patterns different to the normal ones implicit in the traditional reaction-diffusion framework.

6.1 Motivation

The dispersal of organisms is a topic of much importance in Biology due to phenomena such as biological invasions and spread of diseases. A reaction-diffusion approach has traditionally been applied to model this kind of problems. As far as populations mixed for reproductive mode are concerned, Britton and Mogie (2001) have results from a one-dimensional reaction-diffusion equation that show: (1) that the coexistence of sexual and asexual relatives is not possible and (2) that male function in asexuals has a density-dependent effect on the dynamics of mixed populations, favouring the resident against a rare invader. The speeds of invasion that they obtain, however, could not explain the observed geographic pattern of the distribution of sexual and asexual forms. Neither could the modification of their model presented in chapter 5 of this thesis, which added long-range dispersal by means of an advection term to simulate wind dispersal of propagules. That modification was introduced because of the hypothesis that the normal distribution implicit in a reaction-diffusion approach could underestimate the speed of a biological invasion. This opinion is shared by a number of authors (Mollison, 1977; Kot *et al.*, 1996) due to the many species that show leptokurtic rather than normal patterns of dispersal (Bateman, 1950; Wallace, 1966; Okubo, 1980; Crawford, 1984; Howe and Westley, 1986; Willson, 1992; Nathan and Mueller-Landau, 2000). Some of these authors (Mollison, Kot *et al.*) argue for the use of integro-difference or integro-differential equations because these models can accommodate a wider range of dispersal patterns, if different redistribution kernels are used. In particular, for populations with discrete non-overlapping generations, the former are more appropriate. Although dandelions do have overlapping generations, they show strong seasonality. Thus, a discrete-time approach could still be considered. In a first sedentary stage, growth and reproduction are observed. Later, in a second vagile state, propagules are dispersed by wind. This also makes the use of integro-difference equations quite suitable. In the literature of ecological models that use integro-difference equations there are two approaches: that of Fife (1979) and Bates *et al.* (1997), where growth and dispersal occur simultaneously, and that of Kot *et al.* (1996), where growth is followed by dispersal. This second approach will be considered in this model. A final observation is that previous works (Britton and Mogie, 2001; chapter 5 of this thesis) reduced the dynamics of a mixed population to the dynamics of the proportions of one of the types in the population, thus implying the dynamics for the other type. By using a system of equations, where each represents the level of one of the types in the population, this model allows for richer behaviour in the interactions between sexuals and asexuals because, in principle, each type can be assigned its own dispersal pattern. This last observation is of biological importance since, in *Taraxacum*, seeds carrying asexual embryos could be heavier than their diploid sexual counterparts and exhibit a different dispersal pattern.

6.2 The model

As before, a population of outcrossing hermaphrodite flowering plants is considered. Within this model population, some individuals are sexual, their number at time t being denoted by $N_s(t)$. These individuals require the fertilisation of eggs produced by the female function. Other individuals in the population are asexual in the female function — their eggs do not require fertilisation to develop into a new individual,— $N_a(t)$ of them being present at a given moment t. It is also assumed that the simplest genetic system determines reproductive mode: one locus with two alleles, s for sexual reproduction and a for asexual reproduction. The gene a for asexuality is the result of a dominant mutation. Therefore, sexual individuals carry genetic information ss, while asexuals are sa. The assumptions made previously concerning asexuals as potential male parents are also made in this model. Thus, asexuals are considered to have retained a certain level of male function and may fertilise the eggs produced by their sexual counterparts. Male gametes produced by asexuals, however, may not be fully viable. They may be sterile or lead to post-zygotic seed abortion. The fraction of inviable pollen produced by asexuals shall be denoted by u, $0 \leq u \leq 1$. The parameters g_s, $0 \leq g_s \leq 1$ and g_a, $0 \leq g_a \leq 1$ will denote the fraction of their viable pollen carrying a gene s or a, respectively. All pollen produced by sexuals is considered viable and carries gene s. Finally, it is again assumed that both sexual and asexual females allocate the same resources k_f, $k_f > 0$ to the production of eggs.

From the first model of temporal dynamics (chapter 2), the expressions that describe the growth of and interaction between the sexual and asexual components of the population are known. They are given by

$$N_s(t+1) = f(N_s(t), N_a(t)) := v_s k_f N_s(t) \frac{N_s(t) + g_s N_a(t)}{N_s(t) + (1-u)N_a(t)} \tag{6.1}$$

and

$$\begin{aligned} N_a(t+1) = g(N_s(t), N_a(t)) := v_s k_f N_s(t) &\frac{g_a N_a(t)}{N_s(t) + (1-u)N_a(t)} \\ &+ v_a k_f N_a(t). \end{aligned} \tag{6.2}$$

These equations, of course, do not account for the spatial distribution of the population in its habitat, which in this model is thought of as a continuous one-dimensional domain. Thus, let $N_s^t(x)$ and $N_a^t(x)$ denote the levels of the sexual and asexual components of the population at the start of the t-th generation. Equations that describe the population in its habitat are given by

$$N_s^t(x) = f(N_s^t(x), N_a^t(x)) = v_s k_f N_s^t(x) \frac{N_s^t(x) + g_s N_a^t(x)}{N_s^t(x) + (1-u) N_a^t(x)} \tag{6.3}$$

and

$$\begin{aligned} N_a^t(x) = g(N_s^t(x), N_a^t(x)) = v_s k_f N_s^t(x) \frac{g_a N_a^t(x)}{N_s^t(x) + (1-u) N_a^t(x)} \\ + v_a k_f N_a^t(x). \end{aligned} \tag{6.4}$$

Notice that the fact that there is no explicit dependence of the maps f and g on x is a first sign of spatial homogeneity in the model. Up to this point only the sedentary stage has been considered. In order to add dispersal to these equations, linear integral operators that register movement of propagules from all sources y to all other points x in the one-dimensional habitat will be used. Together with the growth and sedentary reproduction stage, the following equations are obtained:

$$N_s^{t+1}(x) = \int_{-\infty}^{\infty} k_s(x-y) f(N_s^t(y), N_a^t(y)) dy \tag{6.5}$$

and

$$N_a^{t+1}(x) = \int_{-\infty}^{\infty} k_a(x-y) g(N_s^t(y), N_a^t(y)) dy. \tag{6.6}$$

In these new and final equations, k_s and k_a are the redistribution kernels or contact distributions around which the model is built. They stand for the probability distributions of the distances that sexual and asexual propagules move, respectively. In other words, these kernels describe the probability that an individual at point x has originated from a neighbourhood of diameter dy around a location y. In principle, k_s and k_a could be any functions of the two variables x and y, that is, $k_s(x,y)$ and $k_a(x,y)$. By choosing to make them dependent on the relative distance $x-y$ between two points rather than on their precise locations, further spatial homogeneity is added to the model and it will be dealing with convolution integrals. Thus, it will be investigated if coexistence of sexual and asexual forms could arise only as a result of the interaction between the reproductive types and their dispersal, but not invoking any spatial variation in the habitat.

6.3 Analysis and results

The behaviour of the solutions to one integro-difference equation involving a convolution integral has been characterised by Kot *et al.* (1996) according to the shape of the redistribution kernel. In a previous article, Neubert *et al.* (1995) lay the foundations to analyse a system of two integro-difference equations. In the first of these works, Kot *et al.* (1996), the aim of the authors is to show that the speed of a biological invasion is extremely sensitive to the precise shape of the redistribution kernel, in particular to the tails of the distribution, while in the second, Neubert *et al.* (1995) they aim to show that the conditions for instability of a spatially uniform steady state are not as severe in a system of integro-difference equations as they are in traditional reaction-diffusion approaches. This model and its aims are different, and so the techniques of those works cannot be fully adopted here. However, they still provide a guide to analyse this system of integro-difference equations. In particular, the analysis will strongly rely on the hypothesis that the asymptotic velocity of expansion of a nonlinear differential or integral model is the same as that of its linearization. This is Mollison's *linear conjecture* (1991). Kot *et al.* (1996) propose and use the discrete-time analogue after some results by Weinberger (1978, 1982), Britton (1986) and Murray (1977, 1989).

For a convolution integral

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y) f[N_t(y)]dy,$$

the discrete-time analogue of the linear conjecture would be expressed by

$$N_{t+1}(x) = f'(0) \int_{-\infty}^{\infty} k(x-y) N_t(y)dy,$$

where $N_t(x)$ is the level of a population on a one-dimensional habitat at the start of the $t-$th generation. The growth of the population is described by the nonlinear function f. The works by Weinberger mentioned above prove this result for models with monotonically increasing growth functions, such as (6.1)–(6.2).

It is the aim of this model to investigate the dynamics at the front of the solutions to the following system of integro-difference equations:

$$N_s^{t+1}(x) = \int_{-\infty}^{\infty} k_s(x-y) v_s k_f \left(1 - \frac{g_a N_a^t(y)}{N_s^t(y) + (1-u) N_a^t(y)}\right) N_s^t(y)dy, \qquad (6.7)$$

$$N_a^{t+1}(x) = \int_{-\infty}^{\infty} k_a(x-y) v_a k_f \left(1 + \frac{\mu g_a N_s^t(y)}{N_s^t(y) + (1-u)N_a^t(y)}\right) N_a^t(y) dy. \qquad (6.8)$$

This system has been obtained by noticing that the formulas (6.3) and (6.4) for the nonlinear terms f and g can be rewritten as

$$f(N_s^t(x), N_a^t(x)) = v_s k_f \left(1 - \frac{g_a N_a^t(x)}{N_s^t(x) + (1-u)N_a^t(x)}\right) N_s^t(x) \qquad (6.9)$$

and

$$g(N_s^t(x), N_a^t(x)) = v_a k_f \left(1 + \frac{\mu g_a N_s^t(x)}{N_s^t(x) + (1-u)N_a^t(x)}\right) N_a^t(x), \qquad (6.10)$$

and substituting the expressions (6.9) and (6.10) in the system (6.5)–(6.6). Notice also that in the course of these manipulations the notation $\mu := \frac{v_s}{v_a}$ has been used. In formulas (6.7) and (6.8), $k_s(x)$ and $k_a(x)$ are some given kernels with exponentially bounded tails, which are referred to as flat-tailed. That is, they are kernels possessing a moment-generating function $M_i(\xi) = \int_{-\infty}^{\infty} k_i(x) e^{\xi x} dx$, $i = s, a$, in a neighbourhood around the origin $s \in (-\xi_0, \xi_0)$, $\xi_0 > 0$. Let it be considered that the dispersal patterns of both sexual and asexual forms follow a Gaussian law. That is, the kernels $k_s(x-y)$ and $k_a(x-y)$ are given by the formulas

$$k_s(x-y) = \frac{1}{\sigma_s \sqrt{2\pi}} e^{-\frac{(x-y)^2}{2\sigma_s^2}}$$

and

$$k_a(x-y) = \frac{1}{\sigma_a \sqrt{2\pi}} e^{-\frac{(x-y)^2}{2\sigma_a^2}}.$$

In this case, the corresponding moment generating functions are given by the formulas $M_i(\xi) = e^{\frac{\sigma_i^2 \xi^2}{2}}$, $i = s, a$. It is also assumed that at the initial moment of time, the functions $N_s^0(x)$ and $N_a^0(x)$ are smooth and equal to zero outside some bounded set.

In attempting to study the system (6.7)–(6.8), one would like to investigate the question of existence of monotonic travelling wave-fronts of sexuals and asexuals invading a virgin environment. Being at the front of the profiles of expansion of sexuals and asexuals means considering the points (x_r^s, r) and (x_r^a, r), where r is a chosen small threshold value for the population level that determines its range or extent. In other words, x_r^s and x_r^a are the points in space where the sexual and asexual populations, respectively, are of certain small size r. By the monotonicity assumption, these numbers are uniquely defined. Moreover, they depend on t, as indicated below:

$$x_r^s = \{x | N_s^t(x_r^s(t)) = r\}$$

and

$$x_r^a = \{x | N_a^t(x_r^a(t)) = r\}.$$

How far the sexual and the asexual fronts are determines the character of the wave of invasion. This is given by the quantity

$$z(t) := x_r^s(t) - x_r^a(t).$$

At the range points, the terms

$$v_s k_f \left(1 - \frac{g_a N_a^t(x)}{N_s^t(x) + (1-u) N_a^t(x)}\right)$$

in (6.7) and

$$v_a k_f \left(1 + \frac{\mu g_a N_s^t(x)}{N_s^t(x) + (1-u) N_a^t(x)}\right)$$

in (6.8) can be rewritten as follows:

$$v_s k_f \left(1 - \frac{g_a N_a^t(x_r^s(t))}{r + (1-u) N_a^t(x_r^s(t))}\right)$$

for $x_r^s(t)$, and

$$v_a k_f \left(1 + \frac{\mu g_a N_s^t(x_r^a(t))}{N_s^t(x_r^a(t)) + (1-u) r}\right)$$

for $x_r^a(t)$, respectively. Doing this will allow different cases to be examined, namely those arising when the relative positions and velocities of the sexual and asexual fronts are considered. Then, the possible behaviours of $z(t)$ are as follows: (i) $z(t) \to \infty$ as $t \to \infty$; (ii) $z(t) \to -\infty$ as $t \to \infty$; (iii) $z(t)$ remains bounded as $t \to \infty$. These cases will be considered in turn.

6.3.1 Displacement of one of the types in the habitat

In order to discuss the cases outlined above, let the situation when $\sigma_s = \sigma_a$ be considered first. How do the speeds of advance of sexuals and asexuals compare then? In this case, the standard deviation has the same effect on both speeds. To answer this question, it will be necessary to distinguish several possible scenarios, namely those where sexuals (or asexuals) are the dominant type, to obtain the conditions under which a given dominating tendency is either maintained or reversed.

Let us first consider the case where sexuals are the predominant type. That is, they have spread over a larger range than asexuals have. At the point where the range of sexuals is measured, $N_a^t(x_r^s(t)) << r$. Equation (6.7) may be approximated by

$$N_s^{t+1}(x) = \int_{-\infty}^{\infty} k_s(x-y) v_s k_f N_s^t(y) dy, \tag{6.11}$$

which is an example of the linear problem discussed in detail by Kot *et al.* (1996). Thus, it is known that the limiting wave speed is given by

$$c_s^{max} = \sqrt{2\log(v_s k_f)}. \tag{6.12}$$

Near the point where the asexual component of the population attains its range, $x_r^a(t)$, it can be seen that $r << N_s^t(x_r^a(t))$. This, in its turn, corresponds to the linear problem

$$N_a^{t+1}(x) = \int_{-\infty}^{\infty} k_a(x-y) v_a k_f (1+\mu g_a) N_a^t(y) dy, \tag{6.13}$$

with wave-speed given by

$$c_a^{max} = \sqrt{2\log[v_a k_f (1+\mu g_a)]}. \tag{6.14}$$

If sexuals keep their dominance over the landscape, that is, if $c_a^{max} < c_s^{max}$, then the condition $\mu > \frac{1}{1-g_a}$ is satisfied by the parameters of the model. In this case, it is expected that sexuals will remain the dominant type in the landscape. If, on the other hand, sexuals are the dominant type but asexuals are expanding more rapidly, two scenarios can be envisaged: (a) asexuals 'catch up' with sexuals, their waves of expansion coalesce and produce a combined-invasion wave, or (b) they outpace the sexuals. The first situation cannot be analysed directly. In the latter situation, $N_a^t(x_r^s(t)) << r$ and $r << N_s^t(x_r^a(t))$ would no longer hold, but rather $N_s^t(x_r^a(t)) << r$ and $r << N_a^t(x_r^s(t))$ would. In this case, the behaviour of the sexual front can be approximated by the linear problem

$$N_s^{t+1}(x) = \int_{-\infty}^{\infty} k_s(x-y) v_s k_f \left(1 - \frac{g_a}{1-u}\right) N_s^t(y) dy, \tag{6.15}$$

and the wave speed would be given by

$$c_s^{min} = \sqrt{2\log\left[v_s k_f\left(1 - \frac{g_a}{1-u}\right)\right]}. \tag{6.16}$$

At the asexual front the behaviour can be approximated by

$$N_a^{t+1}(x) = \int_{-\infty}^{\infty} k_a(x-y) v_a k_f N_a^t(y) dy, \tag{6.17}$$

which is also linear and thus the speed of the invasion wave is given by

$$c_a^{min} = \sqrt{2\log(v_a k_f)}. \tag{6.18}$$

Since asexuals have overtaken sexuals, consistency requires that $c_s^{min} < c_a^{min}$. This implies the condition $\mu < \frac{1-u}{g_s}$ on the parameters of the model. For neither sexuals or asexuals to be dominant, but rather witness a combined-invasion wave, it would be expected that $\frac{1-u}{g_s} < \mu < \frac{1}{1-g_a}$. It is easy to see, however, that $\frac{1-u}{g_s} > \frac{1}{1-g_a}$ and therefore this outcome cannot be obtained.

In a completely analogous way, the case when asexuals have colonised more territory than sexuals can also be considered. Posterior situations, where they might have been displaced or may have remained ahead in the invasion of virgin territory, can be explored. It is easy to see that conditions in the parameters are such that only displacement of one of the types is possible. As in the previous case, a co-invasion is not possible. It will be shown in the next section, however, that if the standard deviations σ_s and σ_a are different, then the case (iii) turns out to be possible and is observed in numerical experiments.

6.3.2 Dynamic coexistence of sexual and asexual forms

The analysis of case (iii) (*cf.* section 6.3) is not as direct as were the analyses of cases (i) and (ii), where one of the two types dominates the landscape, given in the previous section. When there is a wave of co-invasion by sexuals and asexuals, one cannot use the approximations to linear problems given in the previous section (*cf.* (6.11), (6.13), (6.15) and (6.17)). The strategy to follow in this case is to write the speeds of the wave of advance of both the sexual and asexual fronts, so that one can calculate how far apart these invading fronts are from each other. In a situation where both types are co-invading, the distance between their populations' extents should remain bounded over time.

In order to implement the strategy described above, it is necessary to consider the speeds of the invading fronts as functions of time in the following manner:

$$c_s(t) = \sigma_s \sqrt{2 \log \left[v_s k_f \left(1 - \frac{g_a N_a^t(x_r^s(t))}{r + (1-u) N_a^t(x_r^s(t))} \right) \right]} \tag{6.19}$$

and

$$c_a(t) = \sigma_a \sqrt{2 \log \left[v_a k_f \left(1 + \frac{\mu g_a N_s^t(x_r^a(t))}{N_s^t(x_r^a(t)) + (1-u) r} \right) \right]}. \tag{6.20}$$

It will be shown next that under certain conditions on the parameters of the problem, that is σ_s,σ_a,v_s,v_a,k_f,g_a, and g_s, there is $\hat{M} > 0$ such that for any time $T > 0$ there is always a time $\hat{t} > T$ at which the inequality $|x_r^s(\hat{t}) - x_r^a(\hat{t})| \leq \hat{M}$ holds. This result is interpreted as a case of 'dynamic coexistence', when in a neighbourhood of the boundary of the virgin territory there will be a piece of invaded territory in which the levels of $N_s^t(x)$ and $N_a^t(x)$ in the population are comparable no matter how late observations are made.

To get an idea of why such a value $\hat{M}$ should exist, assume that the opposite holds. That is, for any $M > 0$ there is a moment in time $T > 0$ such that $|x_r^s(t) - x_r^a(t)| > M$, if $t > T$. That is, the fronts of N_s^t and N_a^t do not get closer than M to each other after this moment of time. We show that this leads to a contradiction. Indeed, choose a large $M_0 > 0$ and fix a moment of time T_0 such that $|x_r^s(t) - x_r^a(t)| \geq M_0$ for any $t > T_0$. We assume first that $x_r^s(t) - x_r^a(t) \geq M_0$ for any $t > T_0$. Next, consider the number

$$\bar{M} = \sup \left\{ M : x_r^s(t) - x_r^a(t) \geq M, \ t > T_0 \right\}. \tag{6.21}$$

Notice that

$$\bar{M} = \inf \{ x_r^s(t) - x_r^a(t), t > T_0 \}. \tag{6.22}$$

Next, let $\tilde{M}$ be such that $\tilde{M} > \bar{M}$. Again, due to the previous assumption, there is $\tilde{T} > 0$ such that $x_r^s(t) - x_r^a(t) \geq \tilde{M}$ for $t > \tilde{T}$, and clearly $\tilde{T} \geq T_0 + 1$ because otherwise we would have $\bar{M} \geq \tilde{M}$.

The time segment $[T_0 + 1, \tilde{T}]$ contains a finite number of time steps and thus among the elements of the set $\left\{ x_r^s(t) - x_r^a(t), t \in [T_0 + 1, \tilde{T}] \right\}$ there is a minimal one achieved at a time step that will be denoted as t_{min}. It is easy to see that in fact $x_r^s(t_{min}) - x_r^a(t_{min}) = \bar{M}$. Indeed, $x_r^s(t_{min}) - x_r^a(t_{min}) \geq \bar{M}$ by definition of the value $\bar{M}$ (see (6.21)). On the other hand, if it is assumed that $x_r^s(t_{min}) - x_r^a(t_{min}) > \bar{M}$, then, due to (6.22), the following inequalities hold: $\bar{M} \geq \min \left\{ x_r^s(t_{min}) - x_r^a(t_{min}), \tilde{M} \right\} > \bar{M}$, which is a contradiction. Hence the equality $x_r^s(t_{min}) - x_r^a(t_{min}) = \bar{M}$ holds.

Apparently, $N_a^{t_{min}}(x_s^r(t_{min})) \to 0$ and $N_s^{t_{min}}(x_a^r(t_{min})) \to \infty$ as the value M_0 is chosen closer to infinity and hence $\bar{M}$ and t_{min} get larger as well, tending eventually to infinity. This argument could be stated more rigorously by considering appropriate sequences $M_0(n)$, $\bar{M}(n)$ and $t_{min}(n)$ that tend to infinity with n. But a rigorous formulation, together with the notation involved, would make the argument too confusing. The limiting expressions for the speeds of the sexual and asexual fronts as $M_0 \to \infty$, are given by

$$c_s(t_{min}) \to \sigma_s\sqrt{2\log(v_s k_f)} \tag{6.23}$$

and

$$c_a(t_{min}) \to \sigma_a\sqrt{2\log[v_a k_f(1+\mu g_a)]}. \tag{6.24}$$

Assume now that the parameters are chosen in such a way that

$$\sigma_s\sqrt{2\log(v_s k_f)} < \sigma_a\sqrt{2\log[v_a k_f(1+\mu g_a)]}. \tag{6.25}$$

Then, due to (6.23) and (6.24), there is a choice of M_0 such that for the corresponding t_{min} the inequality $c_s(t_{min}) < c_a(t_{min})$ holds. But this means that $x_r^s(t_{min}+1) - x_r^a(t_{min}+1) < \bar{M}$, which contradicts the choice of t_{min} as the point where $x_r^s(t) - x_r^a(t)$ attains a minimum value as described above. Thus, the original assumption is wrong.

In the same way, but using the inequality

$$\sigma_s\sqrt{2\log\left[v_s k_f\left(1-\frac{g_a}{1-u}\right)\right]} > \sigma_a\sqrt{2\log(v_a k_f)}, \tag{6.26}$$

it can be shown that the assumption that for any $M > 0$ there is $T > 0$ such that $x_a^r(t) - x_s^r(t) \geq M$ for any $t > T$ leads to a contradiction. Thus, it can be concluded that if the conditions on (6.25) and (6.26) are satisfied, then the distance between the fronts of $N_s^t(x)$ and $N_a^t(x)$, evaluated at times t_n, such that $t_n \to \infty$, is not greater than a certain value M. Or, as stated before, the sexual and asexual fronts do not get arbitrarily far apart, no matter how late observations are made.

To ensure that there is a propagation of solutions to infinity, corresponding to an indefinite invasion of virgin territory, it must also be required that the values of the speeds are positive at all times t. It is easy to see from the expressions for the speeds in (6.19) and (6.20) that $c_s \geq \sigma_s\sqrt{2\log[v_s k_f(1-\frac{g_a}{1-u})]}$ and $c_a \geq \sigma_a\sqrt{2\log(v_a k_f)}$. Therefore, two other conditions are imposed on the parameters of the model as follows:

$$v_s k_f \left(1 - \frac{g_a}{1-u}\right) > 1 \tag{6.27}$$

and

$$v_a k_f > 1. \tag{6.28}$$

Summarising, if the conditions (6.25)–(6.28) are satisfied, then the situation of dynamic coexistence must occur, as described above.

It is important to note that if this was a continuous-time model, then even more could be said. Namely, that under the same conditions on the parameters of the problem, there is $\hat{M} > 0$ such that the inequality $|x_s^r(t) - x_a^r(t)| \leq \hat{M}$ holds for any t. To see this, consider the continuous-time version of the system (6.5)–(6.6), given by

$$\frac{\partial N_s(t,x)}{\partial t} =$$
$$\int_{-\infty}^{\infty} k_s(x-y)\left[v_s k_f\left(1 - \frac{g_a N_a(t,y)}{N_s(t,y)+(1-u)N_a(t,y)}\right) - 1\right] N_s(t,y)dy$$

and

$$\frac{\partial N_a(t,x)}{\partial t} =$$
$$\int_{-\infty}^{\infty} k_a(x-y)\left[v_a k_f\left(1 + \frac{\mu g_a N_s(t,y)}{N_s(t,y)+(1-u)N_a(t,y)}\right) - 1\right] N_a(t,y)dy.$$

Assume now that there are sequences $M_n \to \infty$ and $t_n \to \infty$ such that $|x_s^r(t_n) - x_a^r(t_n)| \geq M_n$. Then, by choosing an appropriate subsequence $\{n_k\}$, it can always be ensured that either $x_s^r(t_{n_k}) - x_a^r(t_{n_k}) \geq M_{n_k}$ or $x_a^r(t_{n_k}) - x_s^r(t_{n_k}) \geq M_{n_k}$. Let it be assumed, for example, that $x_s^r(t_{n_k}) - x_a^r(t_{n_k}) \geq M_{n_k}$, and change to the index n instead of n_k for simplicity. That is, $x_s^r(t_n) - x_a^r(t_n) \geq M_n$. By introduction of the sequence of moments of time τ_n

$$\tau_n := \inf\{t : x_s^r(t) - x_a^r(t) \geq M_n\}, \tag{6.29}$$

then $N_a(\tau_n, x_r^s(\tau_n)) \to 0$ and $N_s(\tau_n, x_r^a(\tau_n)) \to \infty$. By taking the limits of the speeds of the sexual and asexual fronts, the following relations are obtained:

$$c_s(\tau_n) \to \sigma_s\sqrt{2\log(v_s k_f)}$$

and

$$c_a(\tau_n) \to \sigma_a\sqrt{2\log[v_a k_f(1+\mu g_a)]}$$

as $n \to \infty$.

Assume now that parameters are chosen in accordance with inequality (6.25). Then, there exists n_* such that

$$c_s(\tau_{n_*}) < c_a(\tau_{n_*}). \tag{6.30}$$

But this contradicts the definition of τ_{n_*} given by (6.29).

In an analogous way, it can be shown that satisfying inequality (6.26) makes sure that there is no subsequence $\{n_k\}$ such that $x_r^a(t_{n_k}) - x_r^s(t_{n_k}) \geq M_{n_k}$.

It remains unclear if the stronger result for the continuous-time model holds in the discrete-time case. The results of numerical experiments strongly suggest that it does but it has been difficult to prove this rigorously. The above proof of the continuous-time statement cannot be 'translated into the discrete language' for inequality (6.30) does not contradict (6.29) in the discrete setting. Thus, finding a proof for the stronger statement remains a task for the future.

Notice that in the case when $\sigma_s = \sigma_a$, the conditions (6.25)–(6.28) cannot be satisfied altogether since the inequalities (6.25)–(6.26) are incompatible, which is in accordance with the observations in the previous section. However, the conditions (6.25)–(6.28) define a non-empty set in the parameter space of the model. Of course, this set lies outside those values where $\sigma_s = \sigma_a$. This, in the opinion of the author, is an important feature of the novel treatment given to dispersal aspects. Examples of all possible outcomes, with the corresponding parameter values, are given in figures 6.1, 6.2 and 6.3.

6.4 Leptokurtic patterns of dispersal

The model in this chapter was suggested by the need to reflect long-range dispersal of propagules in a realistic manner. Authors that have studied the dispersal patterns of propagules (*e.g.* Nathan and Mueller-Landau, 2000) agree that the amount of long-range dispersal that takes place is very important for the spread of a population. They also coincide in signalling leptokurtic distributions as a more appropriate way to describe dispersal of propagules.

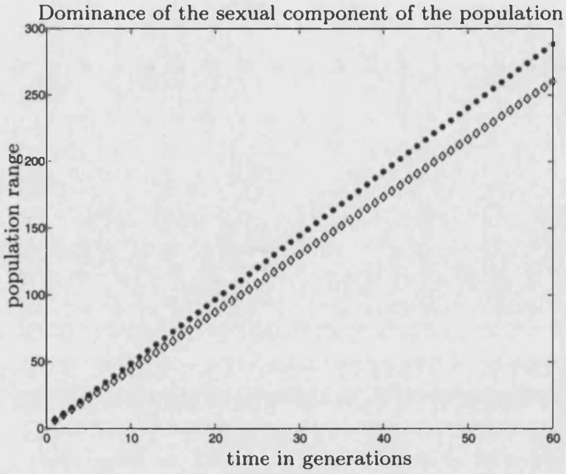


Figure 6.1: The simulation shown in the figure is of an example where the sexual component of the population (*) is clearly spreading faster. The dispersal values are $\sigma_s = \sigma_a = 1$ and $\mu = 3$, with viabilities $v_s = 0.9$ and $v_a = 0.3$. Sexuals (*) eventually are dominant in the habitat. Asexuals are symbolised by ($\Diamond$).

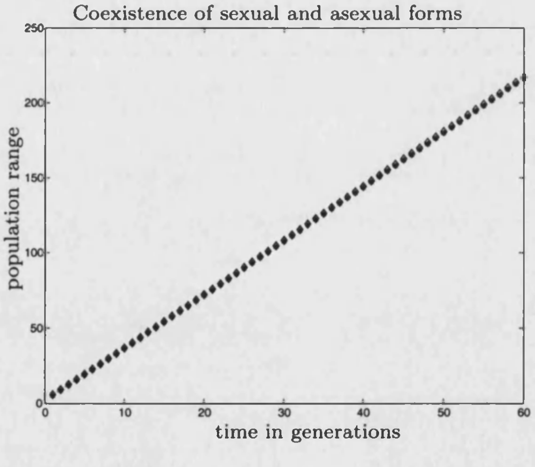


Figure 6.2: In this figure, a co-invasion of sexuals (*) and asexuals ($\Diamond$) is possible because their dispersal patterns are not identical. In this example the parameters are set as follows: $\sigma_s = 0.8585$, $\sigma_a = 0.1$ and $\mu = 3.15$, (μ derives from $v_s = 0.5$ and $v_a = 0.1587$).

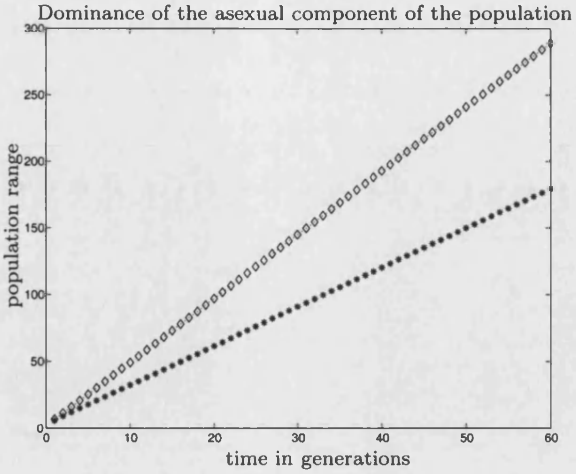


Figure 6.3: The figure shows the asexual component of the population (symbolised by ◊) clearly dominating when dispersal of both types is equal, $\sigma_s = \sigma_a = 1$ Other parameter values are: $\mu = 0.3$, $v_s = 0.3$ and $v_a = 0.9$. Sexuals are represented by the symbol (*).

A general form for dispersal patterns, proposed by Crawford (1984), is given by:

$$y = y_0 \mathrm{e}^{-bx^{1/a}},$$

where a is a parameter that determines the kurtosis of the distribution, while b gives a measure of deviation from the centre of the distribution. If $a < 0.5$, the distribution is platykurtic (thin-tailed); if $a > 0.5$, then leptokurtic (fat-tailed) patterns are obtained. The Gaussian distribution is the special case corresponding to $a = 0.5$. As mentioned before, it is given by

$$y = \frac{1}{\sigma(2\pi)^{1/2}} \mathrm{e}^{-\frac{1}{2\sigma^2}x^2},$$

where $b = 1/(2\sigma^2)$. One advantage of the integro-difference framework is that the dispersal kernels may be readily substituted by their leptokurtic counterparts in formulas (6.7) and (6.8). The disadvantage, however, is that the analysis is not easy to tackle. This part of the work relies completely on numerical simulations, which for completeness are presented in figures 6.4, 6.5 and 6.6. Two features are visible in the leptokurtic system: (a) the speeds of spreads have increased with respect to Gaussian dispersal, and (b) coexistence is also possible.

The following two figures show examples of simulations where one or the other type is eventually excluded from the habitat. When compared to figures 6.1 and 6.3, it is clear that the speeds of spread in the system with leptokurtic dispersal have increased.

The following figure shows examples of coexistence for both Gaussian and

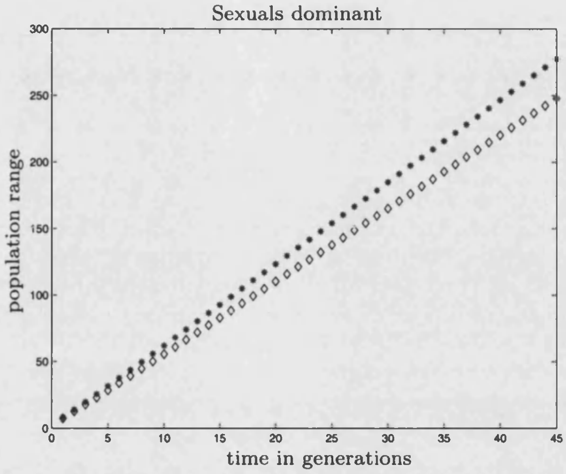


Figure 6.4: The simulation shown in the figure is of an example of leptokurtic dispersal ($a = 0.6$) where the sexual component of the population (*) is clearly spreading faster. The dispersal values are $\sigma_s = \sigma_a = 1$ and $\mu = 3$, with viabilities $v_s = 0.9$ and $v_a = 0.3$. Asexuals are symbolised by ($\Diamond$).

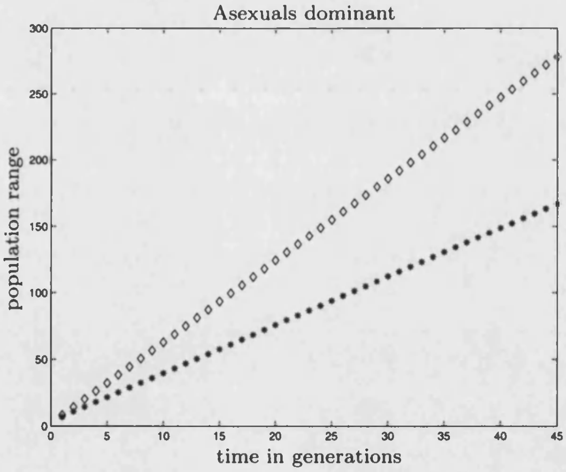


Figure 6.5: The simulation shown in the figure is of an example of leptokurtic dispersal ($a = 0.6$) where the asexual component of the population ($\Diamond$) is clearly spreading faster. The dispersal values are $\sigma_s = \sigma_a = 1$ and $\mu = 3$, with viabilities $v_s = 0.3$ and $v_a = 0.9$. Sexuals are symbolised by (*).

leptokurtic dispersal. In both cases, the sexual and asexual fronts advance very closely, as shown by the graphs of population ranges against time.

6.5 Discussion

The motivation behind this last model in the thesis was the hypothesis that the failure of previous models to accurately reflect the behaviour of an invasion of virgin territory by sexual and asexual relatives was due to the use of non-realistic patterns of propagule dispersal, namely the normal distribution implied by traditional reaction-diffusion approaches. Surprisingly, a model using two equations, one for each type in the landscape, but with the same normal distribution of dispersing propagules, has been enough to provide an elusive result: the coexistence of sexual and asexual relatives.

It seems that the previous failure to find coexistence using one-dimensional dynamical systems lies, in view of the above, on the implicit assumption that $\sigma_s = \sigma_a$ in them. Therefore, the above coexistence result is a strong consequence of the way this model describes the dynamics for each type in the landscape, in the sense that the variables $N_s^t(x)$ and $N_a^t(x)$ in the two-dimensional dynamical system interact in a rather harmonious manner due to the structure of the nonlinearities in (6.5)–(6.6). This model can be manipulated in such a way that only one reproductive mode dominates, but also allows for the 'dynamic coexistence' of both types. All that has been described in the analysis of the model has been confirmed by results from independent numerical experiments, as shown in the figures included in this chapter.

Although it was clear that coexistence does not depend on the pattern of dispersal, simulations with leptokurtic dispersal of propagules are necessary due to the biological relevance of this kind of dispersal. Preliminary results show that the speed with which a population spreads is indeed greater than the one given by Gaussian dispersal only. However, due to the complexity of the equations, little can be said about the value of such speed or the long term behaviour of the front of spread.

6.6 Future work

The proposed system of integro-difference equations is difficult to analyse, especially in case (iii) and when leptokurtic kernels are used. This, however, suggests an important line for future research, one that illustrates the interaction be-

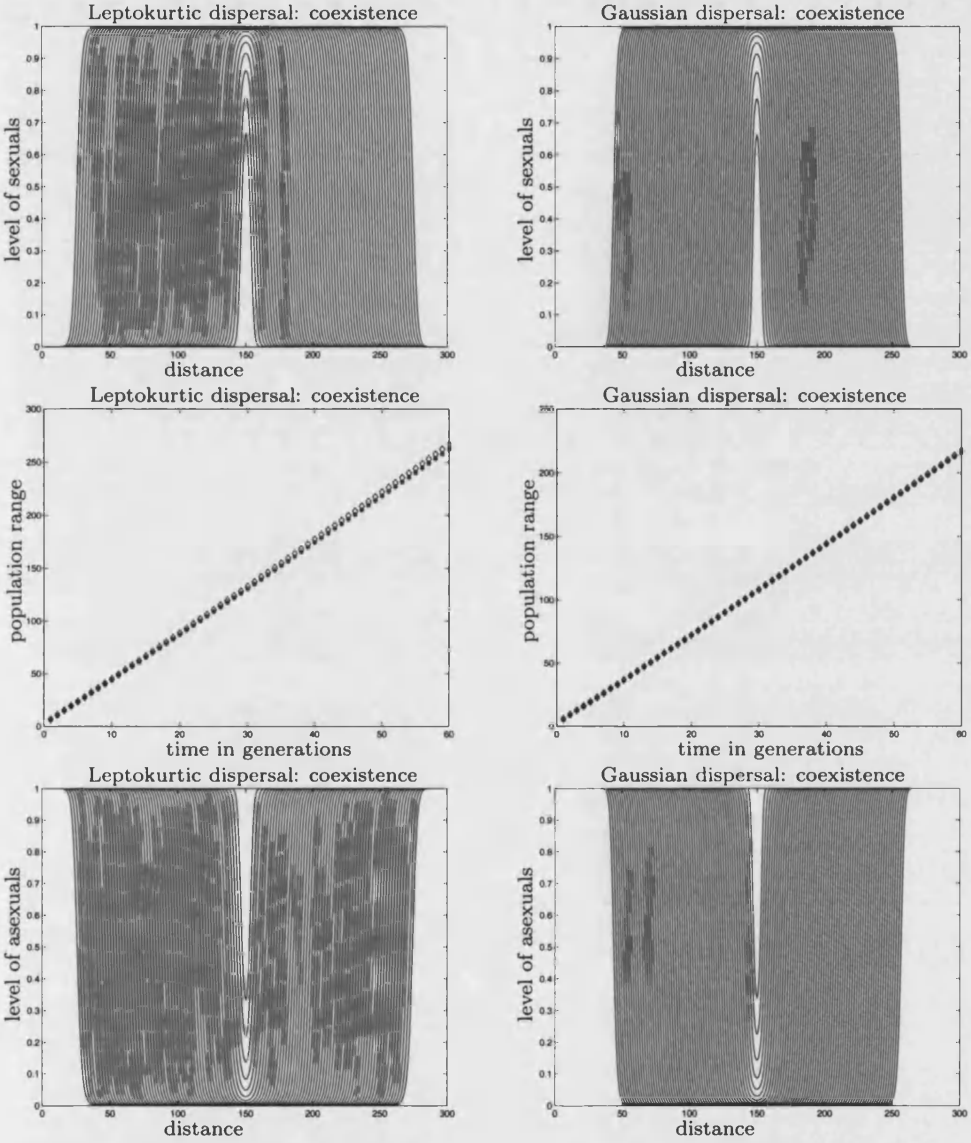


Figure 6.6: The figure shows a comparison of coexistence in the integro-difference system with leptokurtic (panels on the left) and Gaussian (right panels) dispersal. The systems behave similarly, but it is clear that leptokurtic dispersal accounts for faster spread. The parameter values for these simulations are $\sigma_s = 0.8585$, $\sigma_a = 1$, $v_s = 0.5$ and $v_a = 0.1587$. The leptokurtic pattern has been created using $a = 0.6$, while the Gaussian pattern corresponds to $a = 0.5$, as is known from the theory. In the time *vs.* population range plots, sexuals are represented by (*) and asexuals by ($\Diamond$).

tween Biology and Mathematics rather beautifully: not only is it expected that mathematical models shed some light over biological problems, but also the complexity of biological situations in the real world makes one realise that the box of mathematical tools is not yet complete. In this case, the analysis of nonlinear integro-difference equations needs to be generalised. This work easily becomes the subject of a post-doctoral project, as it requires the research experience provided by postgraduate studies.

Returning to the matter of modelling itself, the model in this chapter has also suggested that the decision about the best approach to model a given system is important. In this case, the results of the model suggest that rather than to the chosen mathematical tool, previous failure could have been due to the fact that the sexuality *vs.* asexuality issue had been treated using only one PDE. This imposed the behaviour of one of the types in the landscape on the other. To test this hypothesis, the reaction-diffusion model proposed in chapter 5 could be extended to a two-dimensional dynamical system consisting of two PDEs. This extended model is given by

$$\frac{\partial N_s}{\partial t} = f(N_s, N_a) + D_s \left(\frac{\partial^2 N_s}{\partial x^2} + \frac{\partial^2 N_s}{\partial y^2} \right), \tag{6.31}$$

$$\frac{\partial N_a}{\partial t} = g(N_s, N_a) + D_a \left(\frac{\partial^2 N_a}{\partial x^2} + \frac{\partial^2 N_a}{\partial y^2} \right), \tag{6.32}$$

where D_s and D_a are the diffusion coefficients of sexuals and asexuals, respectively. The growth terms $f(N_s, N_a)$ and $g(N_s, N_a)$ are given by

$$f(N_s, N_a) := v_s k_f N_s \frac{N_s + g_s N_a}{N_s + (1-u) N_a}$$

and

$$g(N_s, N_a) := v_s k_f N_s \frac{g_a N_a}{N_s + (1-u) N_a} + v_a k_f N_a.$$

Notice that this model is not a 'translation' of the integro-difference (ID) model to the reaction-diffusion framework. Indeed, the two models operate in completely different ways. In the integro-difference approach, population growth takes place first and then dispersal occurs. In the PDE model, dispersal and growth occur simultaneously. The PDE model has been written to test if, using two equations, the biological system is better described, even within the reaction-diffusion framework, than it was when only one equation was used as in Britton and Mogie (2001) and chapter 5 of this thesis.

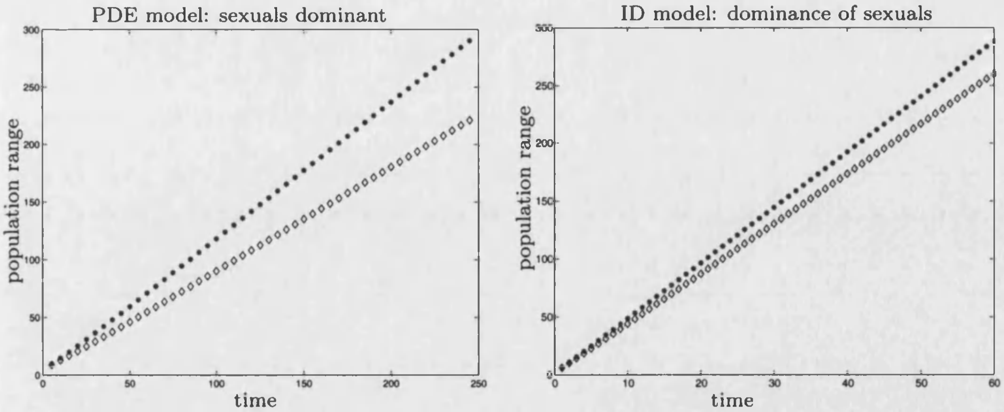


Figure 6.7: The simulation shown in the figure compares the pattern of spread of sexuals (*) and asexuals (◊) in the model consisting of two PDEs (left panel) to the ID model (right panel). In both models, the sexual component of the population is clearly spreading faster. However, it is evident that both populations spread much faster in the ID model. Parameter values are $\sigma_s = \sigma_a = 1$ and $\mu = 3$, with viabilities $v_s = 0.9$ and $v_a = 0.3$. Profiles are plotted every 2.5 time units.

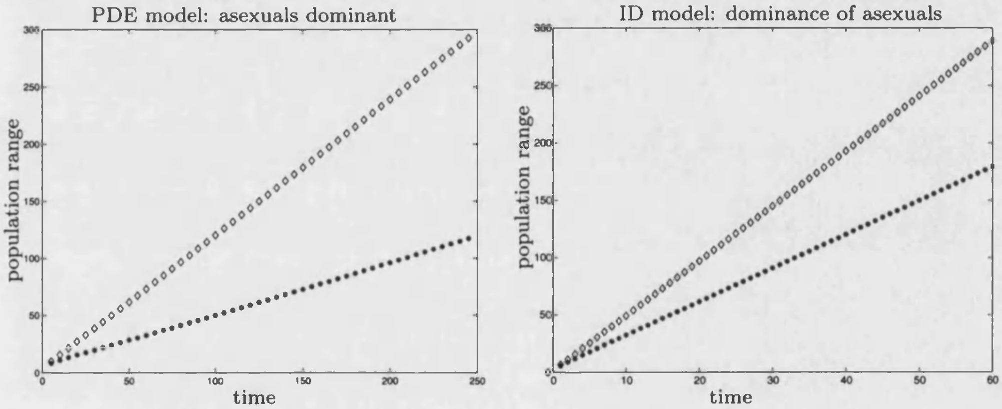


Figure 6.8: The figure is another example of a run of the system of PDEs, only this time asexuals (◊) are dominant. Parameter values are $\sigma_s = \sigma_a = 1$ and $\mu = 0.3$, with viabilities $v_s = 0.3$ and $v_a = 0.9$. Profiles are plotted every 2.5 time units. In these simulations, it is also clear that rates of spread are greater in the ID framework.

Taking these fundamental differences into account, the models were compared numerically. Parameters were set in such a way that the PDE system simulated situations equivalent, in terms of dispersal, to those shown in the ID model. Preliminary results suggest that the use of convolution integrals is more appropriate than the reaction-diffusion approach, even when a system of PDEs is used. The first observation that supports this statement is that rates of spread are slower in the PDE system than in the ID system. In chapter 5, it was discussed that one of the drawbacks of the RD approach was underestimated rates of spread. The PDE system also presents this problem. Examples of spread in the PDE system are given in figures 6.7, 6.8, where it is easily seen that the components of the population in this system spread slowly.

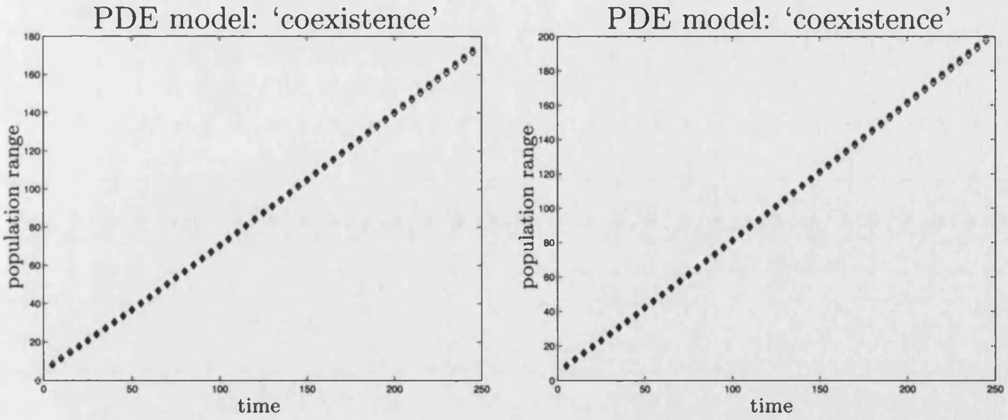


Figure 6.9: The figure shows two simulations of the system of PDEs where the sexual and asexual fronts expand closely for several generations. In both examples, however, sexuals will dominate in the long run. For the simulation on the left, sexuals and asexuals do not have the same diffusion coefficient. For this simulation, $\sigma_s = 0.8585$ and $\sigma = 1$; they have the same diffusion coefficient in the simulation on the right: $\sigma_s = \sigma_a = 1$. In the PDE model, coexistence is an improbable result.

A second observation is that coexistence does not seem to be among the possible results of the PDE model. In fact, numerical simulations suggest that the PDE moel recovers the behaviour of classical models: only one type dominates and eventually displaces the other type from the habitat. Sometimes the dominance of one type over the other is not evident, but in the long run, the dominant type excludes the other. This behaviour is reminiscent of that observed in the CA model, where, even though both types could persist in the landscape for extended periods of time, eventually one of them disappeared. The example offered here shows how sexuals and asexuals can spread almost simultaneously, but with a tendency for one type to dominate. In contrast to the ID, not even assigning different diffusion coefficients to each type seems to promote coexistence. It would even seem that these cases correspond to what was termed "dynamic coexistence" in the ID model, but a closer examination of the data reveals that one of the types will exclude the other. Figure 6.9 shows examples of "coexistence" in the PDE model. In both of these examples, sexuals eventually dominate the population. Moreover, finding these "coexistence" examples is very difficult, which indicates that even if there was a true coexistence point in the parameter space, it would be unstable. Coexistence is thus an improbable result.

Another hypothesis that arose from the ID model was that there may be a relation between the ID system with Gaussian kernels and the PDE system with the traditional Laplacian operator describing diffusion; that there must be a way to recover one from the other, so to speak. But when equivalent situations were studied in one system and the other, they did not seem to show the same behaviour. More theoretical work is needed to understand how solid these observations are. So far, they are backed by numerical comparison of the model and not by an analytic study of the frameworks in which they are inscribed. The theory of PDEs and IDs are active mathematical areas. PDEs and IDs are both applicable to biology. Further knowledge of their theory is needed to understand the differences between these two approaches; particularly, one should understand their limitations and advantages as mathematical tools in Biology.

General Discussion

This is the moment to reflect upon the contributions of this piece of research to the problem that it set out to investigate six chapters ago: the coexistence of sexual and asexual forms within a species in the context of a population of hermaphrodite flowering plants. Since the coexistence of sexual and asexual forms is a wide topic and examples span across the Plant and Animal Kingdoms, at least, constraining the research to a particular group was not only convenient but also advisable. The choice, however, could not be more fortunate: most reported asexual forms among the flowering plants are descended from hermaphrodite, sexual, ancestors. In many cases, they not only coexist with their sexual counterparts, they also interact reproductively with them via the male function that many have retained. The choice was also fortunate from the modelling point of view. Given that previous mathematical models overwhelmingly predict the displacement of one of the forms of reproduction in populations where they are both present, this thesis advocated for a revision of the methodology, namely for wider inclusion of the spatial aspects of the ecology of mixed populations. In this respect, plants, sessile organisms, are a system where the spatial component cannot be ignored. Due to their immobility, they interact successfully only with a limited number of individuals that are 'close' to them. The use of quotation marks is due to the fact that the definition of the effective ecological or genetic neighbourhood in populations remains a challenge. What this concept may represent varies enormously from one system to another. But, back to flowering plants, when one considers processes such as fertilisation by pollen and dispersal of propagules —the only vagile state in the life history of these populations—it is obvious that space is a key factor to be considered in models. It was precisely this factor that had been consistently ignored in models of sex (the exceptions being Keeling and Rand, 1995 and Britton and Mogie, 2001).

The thesis began with a model where only temporal dynamics of a mixed population were considered. A reader familiar with mathematical models of the cost of sex could easily realise that this first, non-spatial model, does not offer results qualitatively different to those of preceding works. Namely, the model also predicts that only one type, sexual or asexual reproduction, can prevail. However, apart from being a summary of previous, well-known models on the advantages and disadvantages of sexual reproduction (Maynard Smith, 1971; Charlesworth, 1980), there is novelty in the approach of the model. This resides in the careful consideration of the biological assumptions to be made. In particular, male function in asexuals is given centre stage. This process is very important in flowering plants because asexuals commonly retain a hold on sexuality by being able to fertilise the eggs of sexual females. Some of the products of this reproductive interaction will be asexual. Apart from the loss of reproductive resources that this represents to the sexual component of the population, new genotypes may be incorporated into the gene pool of asexuals. Despite the apparent advantages and handicaps for one and the other type, the analysis of this temporal-dynamics model gives conditions under which sexuals or asexuals will be the dominant type and eventually displace the other. Perhaps the most important contribution of this first model is to show that a model of its nature, no matter how detailed in the biology, has no scope for results other than those already obtained by previous works. It reinforces the idea that the spatial paradigm should be considered.

Of the many ways in which space has been brought into ecological modelling in recent years, the research chose to try an implicit approach first. Previous experience of the author also played a role in the election of a patch-occupancy model as a first spatial model. It is well known that these models, sometimes referred to as metapopulation models, have been of help to explain phenomena that seem contradictory or that other approaches had failed to capture, such as the coexistence of competing species. They have done so by allowing the weaker competitor to survive globally in patches that open to colonisation, which is not possible in non-spatial approaches. The extent to which sexual and asexual relatives may be considered competitors is not clear, but patch-occupancy models are also useful when studying species diversity (although in this case it would be type diversity). And the choice proved fruitful: stable coexistence of sexual and asexual relatives is among the possible results of the new model. It is also robust to the introduction of biological detail, as was done in the extended model with male function in asexuals. It is the comparison of the two versions of the model with respect to colonisation that may give more light over its success. Originally, a Poisson process is proposed to model the dispersal of propagules to empty patches. The resulting equations are difficult to analyse and thus a modification of the model, a simpler version where colonisation is a uniform process, was studied. The main difference between these two approaches is that the first favours the rarer type, as the rate of colonisation is a decreasing function of the fraction of patches occupied by a given type. In the simpler model, a uniform probability of colonisation gives a constant rate to this process, regardless of the degree of representation, measured in the fraction of patches in the landscape occupied by a given type, a form of reproduction may have in the population. In this second case, the disadvantages intrinsic to each reproductive strategy take their toll, as is made evident by the fact that there is not stable coexistence among the possible results of the simplified model. In the original model, a respite is given to the weaker type in the form of space open to colonisation. In this sense, the weaker competitor would seem to be maintained in the landscape by a sort of fugitive-species tactic. Finally, one must not lose from sight the fact that the major asset of this model resides in the fact that it has shown that different modelling frameworks may change results dramatically and that it pays to diversify, or rather 'spatialise'.

In spite of the encouraging results obtained with the implicit introduction of space, it was necessary to consider other types of spatial model. This search was motivated by one of the most important aspects of the ecology of populations of flowering plants: the dispersal of pollen by insects. It has been shown that insects do not move very far in their foraging. In some species, they may visit as many as six or eight flowers and thus pollen exchange occurs only among close neighbours. This system is not well mixed. The assumption of random mating in the temporal-dynamics model, or the assumption that all other patches (individuals) are equally accessible, were not to be made if the dynamics of fertilisation was to be accurately reflected in the model. Accuracy in the incorporation of detail is perhaps one of the characteristics that have made cellular automata (CA) one of the preferred tools in spatial ecological modelling. The ease of the simulation of this kind of model in a computer, plus the rapid improvement of computing facilities, may be the reason why the use of CA has extended enormously over the last 20 years. For all these reasons, it was the modelling tool chosen to incorporate the detailed mechanics of pollen dispersal in the models of the population under study. Only the eight nearest cells around an individual provide pollen for fertilisation or space for colonisation. There is one qualitatively significant result: sooner or later one type dominates the landscape. This apparent set back is explicable in terms of the mechanics of such a model. It gives rise to spatial configurations where individuals of the same type form clumps. If this could be beneficial for sexuals in terms of pollen donation, it may be heavily counterbalanced by the lack of empty space, territory where the propagules produced at fertilisation would settle. This is made evident by the comparison between the CA and its corresponding patch-occupancy (PO) (or metapopulation or mean-field (MF)) model. In a clustering situation individuals stand in each other's way. The area of sexual dominance in the mean-field model is greatly reduced in the CA. This is certainly explained by the reduction in the colonisation rate. This can be not only formally proved, but also reinforced by simulations of the CA where colonisation is allowed to take place in a 25-cell neighbourhood, while fertilisation remains restricted to the original 8-cell neighbourhood. This modified model is closer to the MF and exhibits a wider area of sexual fixation. It also exhibits stable coexistence, although not at the levels of a MF model. In a restricted CA scenario, sexuals recover all their old disadvantages. As restrictions are loosened, they recover strength. However, the model is not a failure in terms of explaining the coexistence of sexual and asexual forms. It also exhibits several instances of parameter conditions in which, although dominance eventually takes place, coexistence of both types is observed during thousands of generations. These lengthy periods of coexistence may well expand over the calculated duration of an interglacial period before the displacement of one of the types is witnessed. These results are in accord with the hypothesis that sexual and asexual forms are pushed towards the tropics when a glaciation occurs and gradually shift their ranges during the interglacial period. They change from sympatric to the pattern that is commonly observed in the northern hemisphere: sexual forms towards the tropics, asexual forms towards the north. Zones where they coexist may have been observed because this process of geographic differentiation, and thus, exclusion of a certain type from certain habitats, may not be completed even after thousands of years.

The CA model gave fruitful results in another aspect of research in mathematical biology. This model was no exception to the well-known fact that CA are easy to simulate but extremely difficult to analyse. Although many useful techniques have been developed, the mean-field approximation among them, they are normally used in continuous-time models. They also have the drawback of taking the modeller back to an implicit spatial approach. In that sense, the technique that offers the best analytic possibilities, while retaining the flavour of the spatial structure of the CA, is that known as pair approximation (PA). Instead of following the behaviour of the state of single cells, the PA studies the changes in the frequencies of the possible configurations of two adjacent sites. The fact that this technique was originally developed for continuous-time models or for a very simple discrete one, was one of the main difficulties encountered in this part of the thesis. It was evident that a generalisation of the PA was to be implemented for this technique to be of any help. The resulting discrete Markov chain model did provide a better approximation to the behaviour of the CA, much better than that of the MF model. Not only does the PA not differ in behaviour from the CA (*i.e.* it does not exhibit stable coexistence where the CA does not, as did the MF), but it also gives a very accurate numerical fit to the actual simulations of the CA. The fact that the PA required a lot of computing work was an indicator that the original model is complicated, sensible to the ways in which one makes assumptions about the biology, and may benefit from a simplification. This is a task for the future, of course. Meanwhile, the lesson is that the modeller sometimes has to sacrifice detail to analytic power and that very often biological situations prompt the development of new mathematical tools.

Another important aspect of the ecology of populations of flowering plants that demanded attention in spatial models was the dispersal of propagules. The distance at which propagules settle from parent plants is determinant in the rate of expansion of a population's range, the adults being immobile. A study of dispersal can also help to examine the geographic patterns of distribution of sexual and asexual forms. Dispersal to new territory has traditionally been modelled by means of a reaction diffusion formalism and the study of the behaviour of travelling wave solutions. This is the approach that immediately precedes the model presented in chapter 5 (see Britton and Mogie, 2001). Some authors criticise this approach because it allows 'nano-individuals' at the front of expansion to effectively invade virgin territory. These micropopulations are not subject to stochastic effects, which is unlikely (see van Baalen and Rand, 1998, and van Baalen, 2000). A more serious criticism is that they differ qualitatively from and numerically underestimate the behaviour of a system (see Mollison's 'attofoxes', 1991 and Jeltsch *et al.*, 1997). This happens in the case of Britton and Mogie's model, where the rates of expansion of the population are too low even to explain the distribution of natural populations. Thus, this thesis put forward the hypothesis that this failure was due to the fact that their model did not incorporate long-range distance dispersal. This hypothesis followed the opinion of experts in dispersal issues, such as Nanako Shigesada (1997), who emphasises the importance of long-range dispersal in the expansion of population ranges and who has shown that some distributions of trees in Japan could not be explained by short-range dispersal alone. Short-range dispersal of a very specific type, a normal distribution for the distances that propagules travel from the parent plant, is implied in a traditional reaction-diffusion approach. Although a normal distribution does account for propagules that travel long distances, their numbers rapidly decrease to zero. This gives a distribution where most propagules will settle not far from the parent and the stand-in-each-other's-way effect may be present again. The reaction-diffusion in chapter 5 proposed to rectify the absence of long-range dispersal by means of an advection term in the equation. This did not give the desired results. Rates of expansion are increased as much as the velocity of the advection term. Even this rise has its limitations: a very high advection speed may cause a recession of the invading front. Results do not differ, neither qualitatively, nor numerically, from those in Britton and Mogie's model. An advection term is not the way to include this aspect.

Failure in the previous model prompted the research to look for ways to accurately reflect long-range dispersal of propagules. A revision of some relevant literature (Crawford, 1984; Okubo and Levin, 1989; Kot *et al.*, 1996; Nathan and Mueller-Landau, 2000) pointed in the direction of leptokurtic patterns of dispersal. Unlike the normal patterns implicit in reaction-diffusion models, leptokurtic patterns take into account a non-negligible number of propagules that travel long distances. A mathematical tool that can easily accommodate different dispersal patterns is found in integro-differential or integro-difference equations. In the new model, a system of two integro-difference equations was proposed to better reflect the dynamics of the two types present in the territory. This has the additional advantage of allowing for differences in the dispersal of sexuals and asexuals, whereas in the previous model they implicitly dispersed in the same way. For simplicity, a Gaussian pattern of dispersal was used. The difference in the dispersal pattern of the types was provided by the standard deviation. This already accounts for the possibility of a wave of invasion in which both sexuals and asexuals move into virgin territory. In other words, this new model allows for the coexistence of sexual and asexual relatives. Also, the rates of spread found were substantially higher than those found in the reaction-diffusion model. Our hypothesis that long-range dispersal would be the determinant factor for success seems to have been misguided. The new model gives very different results, namely coexistence, using a normal distribution of propagules. Its success seems to reside in the fact that it has two equations, each reflecting the behaviour of a component of the population and thus allowing for differences in their dispersal patterns. This is confirmed by the fact that this same system of two integro-difference equations will not exhibit stable coexistence if the dispersal patterns of sexuals and asexuals are identical. In that case, it effectively reproduces the results from the reaction-diffusion approach. An additional satisfaction of this model was that in order to perform a more advanced analysis, it is necessary to generalise the existing theory for this kind of system of equations. The model provided an example where a situation taken from a biological context prompted the need for theoretical advances in mathematics.

Glossary

This is a small glossary containing those terms that appeared in bold italic characters throughout the thesis. A [C] after an entry means that the definition was taken from the Collins Dictionary of Biology. In other cases the definition has been taken from the Penguin Dictionary of Biology, which is indicated by a [P]. Should the given definition come from another source, this is indicated also immediately after it. In all cases, the sources have been detailed in the bibliography of the thesis. If an entry makes use of another term given in the glossary, that term is indicated in SMALL CAPITALS so that the reader may refer to the corresponding entry.

adventitious embryony a form of asexual reproduction where the ZYGOTE equivalent originates from a somatic cell that is part of the ovule in a flowering plant (Mogie, 1992).

androdioecious having male and HERMAPHRODITE flowers in separate plants [P].

anisogamy the state in which the GAMETES are different from each other, *e.g.* male and female. Usually the former is smaller and more active than the latter [C].

apomixis the development of an embryo in plants without fertilisation [C]; (most common in botanical contexts) reproduction which has the superficial appearance of ordinary sexual reproduction (amphimixis), but occurs without fertilisation and/or MEIOSIS [P].

autogamy fusion of nuclei derived from the same ZYGOTE but from different MEIOSES. Includes all forms of self-fertilisation [P].

automixis fusion of nuclei derived both from the same ZYGOTE and from the same MEIOSIS [P].

binary fission reproduction occurring when a single cell divides into two equal parts [C].

clone any of a group of organisms of identical genotype produced by some kind of asexual reproduction and some sexual processes, such as HAPLOID selfing or the inbreeding of a homozygous line [P].

crossing over mutual exchange of sections of homologous chromatids in the first meiotic prophase [P].

dioecious (of plants) having male flowers carried by one individual and female flowers carried by another individual [C]; male and female reproductive organs being borne on different individuals [P].

diploid nuclei (and their cells) in which the chromosomes occur as homologous pairs (though rarely paired up), so that twice the HAPLOID number is present [P].

epistasis interaction between non-allelic genetic elements or their products, sometimes restricted to cases in which one element suppresses expression of another.

eukaryote organisms in whose cell or cells chromosomal genetic material is (or was) contained within one or more nuclei and so separated from the cytoplasm by two nuclear membranes [P].

evolution an explanation of the way in which present-day organisms have been produced, involving changes taking place in the genetic make-up of populations that have been passed on to successive generations. According to darwinism, evolutionary MUTATIONS have given rise to changes that have, through natural selection, either survived in better adapted organisms or died out [C].

gamete (germ cell) HAPLOID cell (sometimes nucleus) specialised for fertilisation [P]; a specialised HAPLOID cell that fuses with a gamete of the opposite sex (or mating type) to form a DIPLOID ZYGOTE [C].

growth the process of increase in size which has three distinct components, (a) cell division, (b) assimilation, (c) cell expansion. The basis of growth is cell division but in order to increase in size, cells must be able to synthesise new structures that are manufactured from raw materials derived from their immediate environment. This is assimilation and it results in increase in cell size [C].

gynodioecious of female and HERMAPHRODITE flowers occurring on separate plants [C] [P].

haplo- prefix denoting single [C].

haploid 1. (of a cell nucleus) containing one of each type of chromosome. **2.** a haploid organism in which the main life stage has cell nuclei with one of each type of chromosome, written as 'n'. Such organisms (*e.g.* fungi, many algae) usually have a brief DIPLOID phase (2n), returning to the haploid state via MEIOSIS [C].

haplo-diploidy form of reproduction that permits females to control the sex and the sex ratio of their offspring. The mother controls the sex of her offspring during chromosome segregation at egg production. She may withhold sperm and thus lay unfertilised eggs (or release sperm and lay fertilised eggs). In some species (*e.g.* wasps, bees and ants), males develop from unfertilised eggs which carry only half of the maternal chromosomal number. This mode of sex determination is known as arrhenotoky. Where females are the HAPLOID sex the phenomenon is called thelytoky (Greenwood and Adams, 1987).

hermaphrodite an individual that functions as both male and female during some part of its life. When this happens at more or less the same time, the individual is referred to as a simultaneous hermaphrodite, while an individual that functions as one sex during some part of its life changing to the other sex later, or that switches back and forth several times in successive reproductive periods, is referred to as a sequential hermaphrodite or sex-changer (Greenwood and Adams, 1987).

heterozygote an individual containing two different allelic forms of the same gene in all DIPLOID cells [C].

isogamy a system where GAMETES of different sexes or mating types are similar in size (Greenwood and Adams, 1987).

meiosis a type of nuclear division associated with sexual reproduction, producing four HAPLOID cells from a single DIPLOID cell, the process involving two cycles of division. Although meiosis is a continuous process, it has been divided into numerous stages (prophase, metaphase, anaphase and telophase) [C]; process whereby a nucleus divides by two divisions into four nuclei, each containing half the original number of chromosomes, in most cases forming a genetically non-uniform HAPLOID set. A necessary aspect of EUKARYOTIC sexual reproduction, for without it fertilisation would usually double the chromosome number every generation. Meiosis ensures that all GAMETE nuclei from DIPLOID parents contain a haploid set of chromosomes. It also ensures, in sexually outbred populations at least, a wide genetic variation between offspring. This results from genetic RECOMBINATION, both random and non-random [P].

mitosis a type of nuclear division by which two daughter cells are produced from one parent cell, with no change in chromosome number [c]. (**katyokinesis**) method of nuclear division which produces two daughter nuclei, genetically identical to each other and to the original parent nucleus [P].

mutation alteration in the arrangement, or amount, of genetic material of a cell or virus [P].

mutation load the extent to which mutation impairs population fitness [P].

niche the fundamental niche is that which a species could occupy in the absence of competitors, while the realized niche is the one to which it is restricted as a result of the presence of competitors and the specific nature of the competitive interaction with them (Begon *et al.*, 1996).

ontogeny the whole course of an individual's development, and life history [P].

outcrossing a mating system in which matings between close relatives do not usually occur [C]; (Bot.) pollination between (normally genetically) different plants of same species [P].

panmixis or **random mating** the selection of mates by chance [C].

parthenogenesis (in animals) the development of an individual from an egg without fertilisation by a sperm. The process occurs mainly in lower invertebrates, particularly insects [C]; development of an unfertilised gamete (commonly an egg cell) into a new individual [P].

polymorphism the presence in a population of two or more morphs, produced when when different alleles of a gene occur in the same population and the rarest allele is not maintained merely by repeated MUTATION [C].

pseudogamy phenomenon where fertilisation or donation of male GAMETES is required for PARTHENOGENETIC/APOMICTIC development of offspring that derive all their genes from their maternal parent [P].

recombination a rearrangement of genes during MEIOSIS so that a GAMETE contains a HAPLOID genotype with a new gene combination [C]; any process, other than mutation, by which an organism produces cells with gene combinations different from any it inherited [P].

reproduction the mechanisms by which organisms give rise to others of the same kind [C]; the production of new individuals [P].

selection the differential rate of reproduction of one phenotype in a population as compared to other phenotypes. Hence an organism that produces more offspring which survive to reproduce than other type is at a 'selective advantage'. The environmental pressures causing selection may be natural (*e.g.* competition for food) or artificial (*e.g.* insecticides) [P].

sympatric (of a population of organisms) occurring together in the same geographical area. The term is used to describe the geographical distribution of organisms that either coincide or overlap [C].

synergy the joint action of two agents, often producing an effect greater than if the two acted separately [C].

syngamy the fusion of GAMETES [C].

zygote cellular product of GAMETIC union. Usually DIPLOID [P].

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