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## Strategy dynamics

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# Strategy Dynamics

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# Introduction





## INTRODUCTION

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In our actions with other individuals, we often design strategies to achieve our goals at minimum cost to ourselves and others. Is it better to take the train or the car at this time of the day? Should I express my opinion openly and risk that it is not heard, or first hear out my colleagues to find out if they agree with me? Should I do my shoppings for Christmas dinner early and risk that some ingredients will spoil, or should I wait to do them at the last minute and risk that some ingredients are sold out? How successful my strategy is, depends on what strategy you have chosen. What strategy you choose, depends on what strategy you think I will choose. Strategy dynamics studies how the strategies chosen in a population change over time, and is the subject of this thesis. It can be conceived on two levels, which we shall both explore:

- the population-dynamical level, on which we deal with changes in the densities of support of strategies in a community due to interactions of individuals of;
- the evolution-dynamical level, where the interest lies in explaining from population-dynamical arguments how a strategy becomes present, disappears, or coexists with other strategies.

On the population-dynamical level we analyse strategy dynamics where strategies occur as opinions are present as opinions in a community of two populations. In each population all individuals adhere (at least momentarily) to a certain opinion, which differs from the opinion supported in the other population. We follow the densities of support for the two opinions in time when the individuals of the two populations repeatedly meet in small groups. Under the influence of a local majority rule and depending on individual behaviour individuals may change their opinion, and we shall study the generated dynamics in opinion support. Opinion dynamics comprises Part I of the thesis.

Part II of the thesis focuses on strategies on the evolution-dynamical level. Here strategies are phenotypic traits such as they are studied in biology. We consider communities of populations in which the individuals of each populations carry the same trait (expressed as a numerical scalar value), and trait values are supposed to differ between the populations. For convenience we assume that all individuals are haploids and that reproduction is clonal. If one of the individuals generates a mutant individual with a slightly different phenotype, this individual, depending on the environment it encounters, either will be able to increase the presence of its phenotype by means of reproduction or it will not and therefore will disappear

and go unnoticed on the evolutionary timescale. In case of increase of the presence of the mutant phenotype, in general the population with the individual that generated the mutant will disappear and be replaced by the mutant population. The number of phenotypes present in the community then remains unaltered, but one of their values is slightly changed. However, under specific conditions the mutant phenotype is able to coexist with all the phenotypes originally present in the community, and the number of phenotypes present in the community then is increased by 1. We shall also derive that in case the mutant phenotype differs sufficiently enough from that of its progenitor, the mutant type and the progenitor type may disappear from the community, thus causing a decrease in the number of phenotypes present in the community. Phenotypic trait dynamics is also known as adaptive dynamics.

Phenotypic changes are underpinned by changes in alleles, while this is clearly not the case for changes in opinion. Despite these differences opinion dynamics and adaptive dynamics have much in common, and the concept strategy is central to both. Before we introduce opinion dynamics and adaptive dynamics in more detail we shall therefore first in a few words focus on the notion of strategy in general.

### 1.1 THE NOTION OF STRATEGY

Historically, strategies are mental constructions related to warfare. A strategy then is a plan, conceived by a ruler, about how to achieve a specific goal, e.g. to win a war or to conquer a certain piece of land. Considerations on the different ways to achieve this goal and the decision-making on which specific way to choose are called tactics. These concepts are reflected e.g. in the ancient game of chess, which abstracts warfare and in which a player uses a strategy (e.g. directing pieces towards the enemy king) and tactics (e.g. winning a pawn on the way) to reach the final goal, which is to mate the opponent's king. Given the connection of strategies with warfare one might be inclined to think that strategies are stated in terms of contrasts, but this is not necessarily the case: in order to reach a certain goal it may well be useful to seek for (temporary) support from or co-operation with other individuals and go to the battlefield together.

Taking an instant leap from ancient times into modern societies one observes that the notion of strategy, now often less bellicose but still concerned with a plan to reach a predetermined goal, is present everywhere: from the world of business to politics, and from sports to science. A main part of the planning has to do with overcoming problems that obstruct the path to the goal. The causes of these problems, or anything that interferes with any path to reach the goal, is considered to belong to the environment of the strategy or the strategist, i.e., the entity (a person, animal, plant, robot) that tries to reach the goal. As such executing a strategy may be conceived as a struggle (but one that may be less dramatic than

it sounds), which resonates e.g. in the 'survival of the fittest' characterisation of Charles Darwin's theory of evolution by natural selection.

The entity that executes the strategy may have a mental representation of the strategy. This will be the case for a general engaged in warfare, a chessplayer trying to win a game, a soccer trainer composing a team for the next match, or an executive of a company who aims to maximise profits. But such an internal mental representation is not a requirement in order to talk about strategies. Consider for instance bees that extract nectar from the flowers they visit. One strategy may involve visiting flowers of a single flowering plant species, whereas another strategy involves visiting flowers of many different flowering plant species. The bees are executing a strategy that is partly learned and partly genetically-based. They will be unaware of their strategy. Also plants are clearly unaware of the strategy they play. Examples of strategies executed by plants are: producing many small seeds for reproduction, or producing only a few large seeds for reproduction. Other strategies involve dealing with stress caused by external disturbances such as predators or lack of food or space. (The discussion of plant behaviour in terms of strategies gained impetus in the 1970s with the publications by Harper and Ogden [44] and Grime [43].) In what follows we shall drop the distinction between entities that are mentally aware of the strategies they execute and those that lack this awareness. By doing so we allow ourselves to use the statement that an entity has, carries, executes or performs a strategy. For convenience we shall also loosely switch between the use of 'strategy' and those that execute, carry or perform the strategy.

As stated above, in trying to reach the goal as planned by a strategy in general obstructions have to be tackled. These obstructions belong to the environment in which the strategy is executed, and in this environment entities executing other strategies may be present, thus leading to various possible interactions of strategies. In general this interaction will change the density of support for both strategies. In case that two strategies interact, the most extreme cases are complete competition, in which both strategies go for their own goal with disadvantage for the other strategy (i.e. a decline in density or per capita growth rate for the support of both strategies), or a complete co-operation in which each strategy profits from the presence of the other strategy (expressed by an increase in density or per capita growth rate for support of both strategies). Any other form of interaction classifies as exploitation, in which one strategy profits at the cost of the presence of the other strategy.

Interaction, e.g. competition, of strategies may lead to the replacement of a strategy by one that is more capable or more effective (taking into account certain criteria) to deal with the environment, i.e. the obstructions encountered in realising its goal. It is also possible that under certain conditions two competing strategies coexist. Coexistence of strategies as well as replacement of a strategy due to interaction and the resulting dynamics will be discussed in detail in this thesis.

Mathematicians J. von Neumann and J. Nash formalised thinking about strategies in the so-called game theory, see e.g. [79]. Game-theoretical concepts initially were applied in economics, but turned out to be useful in many fields of science. Maynard Smith applied similar concepts to the field of biology [69], [70]. He introduced the term Evolutionarily Stable Strategy (ESS), which is a strategy which, when common, cannot be beaten by any other strategy. We shall encounter this type of strategy as well as other ones in the discussions of opinion dynamics and adaptive dynamics.

## 1.2 OPINION DYNAMICS

The first strategies that we are considering are opinions. The field of 'opinion dynamics' originated from sociophysics, which applies methods originally used to model physical phenomena to explain social processes. Two early approaches that yielded insight in this respect were lattice models, already used in the 1940s to study social segregation, and the Ising model for ferromagnetism as a first application to understand opinion dynamics (see e.g. [88]). Nowadays sociophysics is a growing field of research with applications covering different such as strike behaviour [31], flock behaviour [19] and fluctuating financial markets (as a specialisation of sociophysics called econophysics; see also [30] and e.g. [88] and [86] for recent overviews). Within the field of sociophysics, opinion dynamics deals with the behaviour of opinion support in communities (see e.g. [10], [21], [24] to get an impression on the subject). In particular we consider communities in which two opinions are present, and we are interested in the dynamics of the support as generated by individuals who have different attitudes with respect to the opinion they support.

In the first chapter of Part I on opinion dynamics a supporter of an opinion may be an inflexible or a floater. An inflexible always maintains the supported opinion, independent of the circumstances encountered. A floater changes opinion in case the initially supported opinion has the minority in the environment it finds itself in. Here the environment consists of groups of three individuals. This environment is repeatedly locally updated by randomly regrouping all individuals into groups of size 3. Thus, due to application of the local majority rule all individuals in a group adopt the opinion that has the local majority in that group. In case all individuals in the community are floaters, the opinion that initially has the majority in the community will fully take over, with opinion support of 50% in the community being a repeller for both opinions. In case only one of the two opinions is supported by inflexibles with sufficiently small density, the outcome of the dynamics due to repeated local updates is governed by two local attractors. On one of these attractors both opinions are present, with the one supported by inflexibles being the minority. On the other attractor the opinion supported by the inflexibles is the only opinion present. This implies that the outcome for the dynamics depends on the initial condition, and we derive that the basin of attraction for the mixed

local attractor is relatively small compared to that for the single opinion attractor. Furthermore we show that in case the density of inflexibles becomes sufficiently large (approximately 17%), the mixed attractor disappears and the single state attractor becomes global.

In case both opinions are supported by equally small densities of inflexibles, there are two mixed local attractors for the dynamics, separated by a repeller on which both opinions are supported by half of the population. As soon as the density of inflexibles become different this symmetry disappears. A sufficiently large increase in density for one of the opinions may lead to a global attractor on which the opinion with the larger density of inflexibles has the majority.

In the second chapter on opinion dynamics we take floaters to show either non-contrarian or contrarian behaviour. A non-contrarian shows the behaviour of a floater as described before, whereas a contrarian floater goes against the grain and subsequently changes its opinion to the alternative one. Contrarian behaviour may represent various kinds of attitudes against one's environment, e.g. an expression for individualisation by adolescents, especially in the presence of inflexible opinion supporters, or an expression of conformity with a minority. We again determine the dynamics of the support for the two opinions, now under repeated local updates for group sizes 1, 2 and 3. Given fixed densities of inflexibles for the two opinions, and fixed fractions of contrarians among the floaters for the two opinions, we derive the dynamics in case individuals meet in groups of either size 1, 2 or 3. We again state conditions, now in terms of these densities of inflexibles and fractions of contrarians, that determine if an opinion will eventually gain the majority. It is shown that relatively small densities of inflexibles allow for various qualitative outcomes (in terms of number of equilibria and monotone vs. alternating dynamics with respect to attractors or repellers), and that an increase in the densities of inflexibles diminishes this variation in dynamics.

### 1.3 ADAPTIVE DYNAMICS

In biology, differences between organisms with different phenotypic traits, for instance offspring size or sex ratio of the offspring, are also referred to as differences between strategies. Phenotypic traits are genetically based, and occasionally new phenotypic traits are produced due to mutations in the DNA. In what follows we shall call a phenotypic trait simply a phenotype.

Alleles present in the individuals of a population will by means of reproduction become available in the next generation. The frequency of an allele in the next generation is determined by its allele fitness, i.e, the relative increase in frequency of the allele from one generation to the next one, and will depend on the selection that the genotypes in which the allele participates experience in the environment these genotypes encounter. A simple population-genetical model illustrates this. Suppose that two alleles  $A$  and  $a$  are present in a population of diploid organisms, with initial frequencies 0.5 for the homozygotes  $AA$ , 0 for the heterozygotes  $Aa$ ,

and 0.5 for the homozygotes  $aa$ . Assuming that  $AA$  has the highest fitness, and that  $aa$  has the lowest fitness, allele  $A$  will outcompete  $a$  as expected. If however the heterozygotes have the highest fitness, all three genotypes and therefore also both alleles will remain present in the population.

In practice allele frequencies and allele fitness as well as the phenotypic realisation of a genotype are hard to quantify. Most of the insights in population genetics and evolutionary genetics are therefore obtained from theoretical mathematical models in which selection is directly on the genotypes under assumption on allele fitness. Also, one could argue that selection is done on phenotypes that are expressions of alleles, and causes changes in phenotype densities in a population and consequently also on allele frequencies. The awareness of this short-cut lead to evolutionary game theory (the 'game'-part gets involved to explain how a strategy in a game should evolve to eventually give optimal profit; e.g. in a strongly female-biased population it would be good for maintenance of the population to produce many sons, whereas in a strongly male-biased population the same strategy will not be successful) and phenotypic optimisation theory, and later to adaptive dynamics (see e.g. [8], [73], [39]). These approaches try to overcome the intricacies of evolutionary genetics by focusing on the changes of phenotypes in time. The advantage obtained by leaving out genetic details is that it facilitates the mathematical analysis of these changes.

Adaptive dynamics assumes a community of populations that is assumed to reside on a community-dynamical attractor in which each population consists of individuals that all have the same strategy, and with different strategies for the individuals of different populations. The phenotypes of the various populations determine the phenotypic trait composition of the community, and are called the resident phenotypes. In such a community of populations a mutant population may occur, generated by one of the populations present in the community. The mutants' strategy therefore is close to that of its progenitor population. An important notion in adaptive dynamics is the invasion fitness of a phenotype. In case the mutant's phenotype has a non-positive invasion fitness it is not capable of increasing its initially infinitesimally small density in the environment as set by the community-dynamical attractor in which it appears and goes extinct, unnoticed on the evolutionary timescale and leaving the community-dynamical attractor unaltered. A positive invasion fitness implies a positive probability for the mutant population to increase its density and to invade the environment as set by the community-dynamical attractor. In case a mutant population invades, its strategy as well as the mutants that carry this strategy are called successful. In case the mutant population does invade, there are three, mutually exclusive, outcomes possible:

1. the mutant population replaces its progenitor population, and together with the remaining populations settles on a new community-dynamical attractor which has a slightly different composition in terms of the phenotypic traits

present on it, thus implying a small shift in the phenotypic trait composition of the community;

2. the appearance of the mutant population causes the extinction of the mutant population as well as of its progenitor population, and on the attractor the community eventually will reach the number of phenotypes present then will be reduced by 1 compared to that number for the invaded attractor<sup>1</sup>
3. the mutant population is able to coexist with all the resident populations. In this case the number of distinct phenotypic trait values present on the community-dynamical attractor eventually reached by the mutant and resident populations is increased by 1 with respect to that number for the invaded attractor.

The assumption made above that a successful mutant population appears in a community that resided on a community-dynamical attractor is motivated by the fact that evolutionary time as set by the pace of the occurrence of successful mutants is much slower than community-dynamical time as set by the times communities need to reach an attractor.

Plotting the phenotypic trait compositions of subsequent community-dynamical attractors on an evolutionary timescale results in a picture that resembles an evolutionary tree. Figure 1.1 shows an example of such a picture for scalar phenotypic trait values. The replacement of a progenitor population by a mutant population corresponds to the growth of a branch of the tree, extinction of the mutants and the progenitor population as a result of invasion agrees with pruning of a branch, and coexistence of the resident populations together with the mutant population corresponds to branching of the tree. E.g., in Figure 1.1 halfway the evolutionary timescale the tree shows that four resident trait values are present, resulting from three branching events in the past. This implies that the community resides on a community-dynamical attractor on which four populations are present, each represented by its phenotypic trait value (which are called here the resident trait values). With the increase of time the branches grow due to subsequent replacements in one of the branches, leaving the other branches unaffected. Eventually one of the branches is pruned, resulting in a community of three populations that continues evolving.

#### 1.4 OVERVIEW

After this introduction, the thesis continues with Part I, in which opinion dynamics is discussed. Chapter 2 considers the effect of inflexibles and floaters on the

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<sup>1</sup> It is to be noted here that the extinction of one population may also cause a cascade of extinctions of other populations present in the community; this is however not the rule. Furthermore, in host-parasite models it may occur that the invasion of a mutant host population does not cause the extinction of its progenitor population but of the parasite population; see e.g. [99].

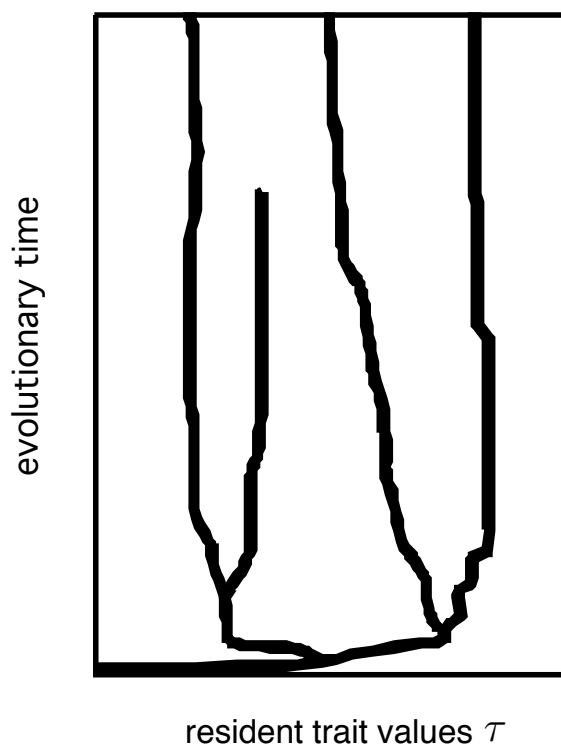


Figure 1.1: Phenotypic trait composition of subsequent community-dynamical attractors plotted against evolutionary time.

densities of two opinions under the local majority rule in groups of size 3. In Chapter 3 this model is extended to include inflexibles as well as non-contrarian and contrarian floaters, and considers besides groups of size 3 also groups of sizes 1 and 2.

Part II turns to adaptive dynamics. As follows from the introduction above, adaptive dynamics studies the subsequent phenotypic trait compositions of attractors that a community visits, where the change from one attractor to the other is caused by the invasion of a successful mutant population. Chapter 4 presents a notion of community-dynamical attractor, and we derive that for a large class of community-dynamical models such an attractor exists. Chapter 5 then discusses adaptive dynamical processes based on Lotka-Volterra community-dynamics. The phenotypic traits are taken to be scalar values and appear as arguments in so-called interaction functions that determine the strength of interaction between individuals of interacting populations. It is derived that in the context of Lotka-Volterra community-dynamics the invasion fitness function can be calculated explicitly, and many results dealing with the outcome of a mutant population invasion can be stated in terms of invasion fitnesses. The three processes that shape the evolutionary tree (trait substitution, evolutionary pruning and evolutionary branching) are analysed in terms of invasion fitness. We also derive that permanence (i.e. the property that all densities in a community of populations stay sufficiently far away from 0 to be present permanently in time) is



maintained under sufficiently small mutational steps. This result implies that for evolutionary pruning to occur a sufficiently large mutational step is required.

The thesis ends with Part III, in which Chapter 6 summarises Parts I and II and discusses a number of open questions.



# **Part I**

## **Opinion Dynamics**



## THE ROLE OF INFLEXIBLE MINORITIES IN THE BREAKING OF DEMOCRATIC OPINION DYNAMICS

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This chapter is based on:

S. Galam and F. Jacobs, The role of inflexible minorities in the breaking of democratic opinion dynamics, *Physica A* 381, 366-376, 2007

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### ABSTRACT

We study the effect of inflexible agents on two state opinion dynamics. The model operates via repeated local updates of random grouping of agents. While floater agents do eventually flip their opinion to follow the local majority, inflexible agents keep their opinion always unchanged. It is a quenched individual opinion. In the bare model (no inflexibles), a separator at 50% drives the dynamics towards either one of two pure attractors, each associated with a full polarisation along one of the opinions. The initial majority wins. The existence of inflexibles for only one of the two opinions is found to shift the separator at a lower value than 50% in favour of that side. Moreover it creates an incompressible minority around the inflexibles, one of the pure attractors becoming a mixed phase attractor. In addition above a threshold of 17% inflexibles make their side sure of winning whatever the initial conditions are. The inflexible minority wins. An equal presence of inflexibles on both sides restores the balanced dynamics with again a separator at 50% and now two mixed phase attractors on each side. Nevertheless, beyond 25% the dynamics is reversed with a unique attractor at a fifty-fifty stable equilibrium. But a very small advantage in inflexibles results in a decisive lowering of the separator at the advantage of the corresponding opinion. A few percent advantage does guarantee to become majority with one single attractor. The model is solved exhaustedly for groups of size 3.

Keywords: Sociophysics, majority rule, opinion dynamics

PACS numbers: 02.50.Ey, 05.45.-a, 9.65.-s, 87.23.Ge

### 2.1 INTRODUCTION

Opinion dynamics has become a very active subject of research [2, 58, 62, 75, 89, 91, 94, 96, 98] in sociophysics [22, 31]. Most works consider two state models which

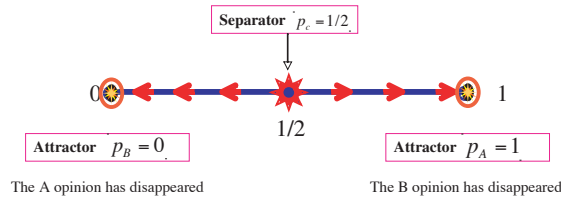


Figure 2.1: The bare model with only floaters. The initial majority is conserved and increased to eventually invade the whole population.

lead to the disappearance of one of the two opinions. They use local updates in odd size groups which result in the initial majority victory. A unifying frame was shown to include most of these models [26]. Continuous extensions [15,56] and three state models [37] have been also investigated.

However, including an inertia effect in even size local updates groups, the initial minority may win the competition spreading over the entire population. The inertia effect means that in an update even size group at a tie, the opinion which preserves the Status Quo is selected locally by all the group members [21,25]. When an opinion represents a vote intention, the model allows to make successful prediction in real voting cases like for the 2005 french referendum [27].

At contrast it is found that including contrarian behaviour leads to the reversal of the dynamics with a stable equilibrium at exactly fifty-fifty whatever the initial conditions are. A contrarian is an agent who makes up its opinion by choosing the one minority opinion, either the local minority within its update group [23] or the global minority according to polls [6]. It was used to explain and predict the occurrence of a recent series of hung elections in democratic countries [23].

In addition to contrarian behaviour [6,20,23,93], another type of behaviour is also quite current while dealing with real opinion dynamics, it is the inflexible attitude. At contrast to floater agents who do eventually flip their opinion to follow the local majority, inflexible agents keep their opinion always unchanged. The inflexible attitude is a quenched individual state. Surprisingly, it has not been studied so far. It is the subject of this article to investigate the inflexible effect on the associate opinion dynamics. To confront our results to any real situation requires to have an estimate of the various densities of inflexibles, which could be extracted in principle from appropriate polls.

In the bare model, where no inflexible is present, denoting A and B the two competing opinions and  $p_t$  the density of A at time  $t$ , the flow diagram of the dynamics is monitored by a separator at  $p_c = 50\%$ . it drives the dynamics towards either one of two pure attractors,  $p_B = 0$  where the A opinion has totally disappeared, and  $p_A = 1$  where the A opinion has totally invaded the whole population. It is shown in Fig. 2.1. The initial majority always wins.

The existence of inflexibles for only one of the two opinions, for instance opinion A, is found to shift the separator at a lower value than 50% in favour of that side. Moreover it creates an incompressible minority around the inflexibles, one of the

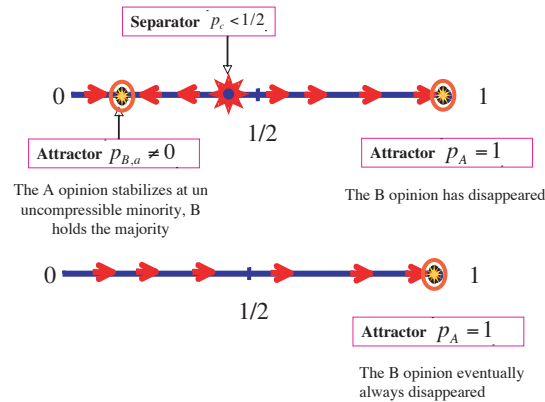


Figure 2.2: One side inflexibles at low density. In the upper part inflexibles shift the separator to a lower value than 50% at the advantage of their side. Moreover, the associated opinion never disappears but at minimum stabilises at some stable minority value  $p_{B,a}$ . The associated opinion can now invade the whole population even when it starts at an initial value lower than 50% within some appropriate range. The lower part shows that beyond 17% in the density of inflexibles, the separator and the mixed phase attractor have vanished after they have coalesced. At any initial condition, A wins and eventually invades the whole population.

pure attractors, here  $p_B$ , becoming a mixed phase attractor, where opinion B holds the majority but with a stable A minority,  $p_B = 0 \rightarrow p_{B,a} \neq 0$ . See the upper part of Fig. 2.2. In addition, increasing the one side inflexible density above some threshold (17% for update group of size 3) inflexibles make the separator and the mixed phase attractor to coalesce and thus cancel each other to both disappear. Their side becomes certain of winning whatever the initial conditions are. The inflexible minority wins as illustrated in the lower part of Fig. 2.2.

However an equal presence of inflexibles on both sides is shown to restore the balanced dynamics with again the separator at  $p_c = 50\%$  and now two mixed phase attractors  $p_{B,a} \neq 0$  and  $p_{A,b} \neq 1$  on each side as seen in the upper part of Fig. 2.3. Nevertheless, beyond 25% the dynamics is reversed with a unique attractor at a fifty-fifty stable equilibrium. See the lower part of Fig. 2.3.

But again, a very small advantage in inflexibles results in a decisive lowering of the separator at the advantage of the corresponding opinion as shown in the upper part of Fig. 2.4. In addition the lower part of Fig. 2.4 shows that a few percent advantage does grant the victory.

## 2.2 GROUP SIZE 3

We now solve analytically the problem for local update groups of size 3. Initial proportions at time  $t$  of both opinion are respectively  $p_t$  and  $(1 - p_t)$  where each agent does have an opinion. On the A side, at any time the associated agents are

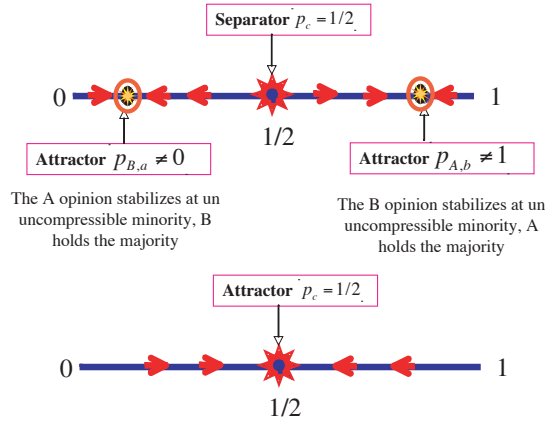


Figure 2.3: Equal presence of inflexibles on both sides. In the upper part the balanced dynamics is restored with the separator back at  $p_c = 50\%$ . Now two mixed phase attractors  $p_{B,a} \neq 0$  and  $p_{A,b} \neq 1$  are located on each side of the separator. Nevertheless, in the lower part, beyond 25% they both coalesce with the separator, which at once becomes the unique attractor. The dynamics is reversed with a coexistence of both opinions at a fifty-fifty stable equilibrium.

divided among a fixed and constant proportion of inflexibles  $a$ , they always keep on opinion A, and a varying density of floaters  $p_t - a$ . The floaters do shift opinion depending on their local update group composition. Similarly, on the opposite side B, the agent holder contains a fixed and constant proportion of inflexibles  $b$  with a density of  $(1 - p_t - b)$  floaters.

Dealing with densities we have the constraints  $0 \leq a \leq 1$ ,  $0 \leq b \leq 1$ ,  $0 \leq a + b \leq 1$  and  $a \leq p_t \leq 1 - b$ . To make the notations more practical we introduce the difference in inflexible densities  $x$  to write  $a \equiv b + x$  with  $-b \leq x \leq 1 - 2b$ . The value of  $x$  may be negative to account for an advantage to the B opinion. A positive value corresponds to an advantage to A. The two external parameters of the problem are thus  $b$  and  $x$ .

Then at time  $t$  people are grouped randomly by three and a local majority rule is applied separately within each local group. At time  $t + 1$  within each group all floaters who held the minority opinion do shift to the local majority one. However inflexibles do not shift their opinion. Dealing with three agents, the only subtle cases are the ones where 2 agents sharing the same opinion are against the third who holds the other one. In case it is a floater the minority agent joins the majority, otherwise being an inflexible, it does shift opinion and keeps the minority opinion. A detailed counting of all cases leads to write at time  $t + 1$  for the new proportion of opinion A,

$$p_{t+1} = p_t^3 + 3p_t^2 \left( (1 - p_t - b) + \frac{2}{3}b \right) + 3(1 - p_t)^2 \left( \frac{1}{3}a \right), \quad (2.1)$$



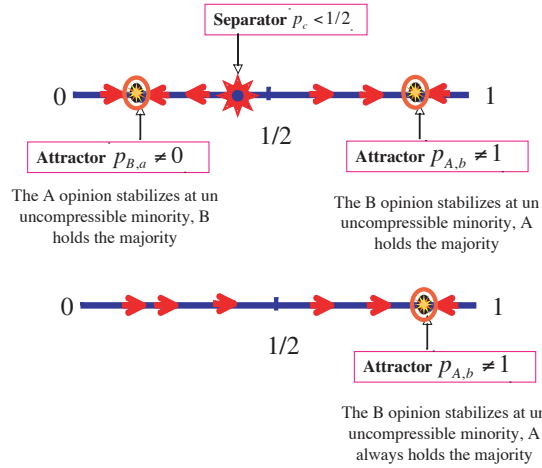


Figure 2.4: Unequal densities of inflexibles. The upper part shows a rather small difference in inflexibles, which results in a decisive lowering of the separator at the advantage of the corresponding larger side. The lower part shows the case of a few percent advantage, which does grant the victory.

which simplifies to

$$p_{t+1} = -2p_t^3 + p_t^2(3 + x) - 2(b + x)p_t + b + x. \quad (2.2)$$

After one update, all agents are reshuffled before undergoing a second redistribution among new random groups of three agents each. Now  $p_{t+1}$  plays the role of  $p_t$  before, and a new density  $p_{t+2}$  is obtained. The process is repeated some number  $n$  of times leading to the density  $p_{t+n}$  of agents sharing opinion A and  $1 - p_{t+n}$  of agents sharing opinion B. It is worth to stress that the respective proportions of inflexibles  $a$  and  $b$  are unchanged and independent of the value of  $n$ .

While the reshuffling frame has been viewed as belonging to a mean field treatment [89,96,98], it has demonstrated to indeed create a new universality class [92].

Before proceeding we review the bare model, i.e., no inflexible is present ( $a = b = 0$ ) and all agents are floaters. From Eq. (2.2) one cycle of local opinion updates via three persons grouping leads to the new distribution of vote intention as,

$$p_{t+1} = p_t^3 + 3p_t^2(1 - p_t), \quad (2.3)$$

whose dynamics is monitored by the unstable fixed point separator located at  $p_c = \frac{1}{2}$ . It separates the respective basins of attraction of the two pure phase stable point attractors at  $p_A = 1$  and  $p_B = 0$ . Accordingly  $p_{t+1} > p_t$  if  $p_t > \frac{1}{2}$  and  $p_{t+1} < p_t$  if  $p_t < \frac{1}{2}$  as shown in Fig. 2.1. The initial majority wins.

For instance starting at  $p_t = 0.45$  leads successively after 5 updates to the series  $p_{t+1} = 0.43, p_{t+2} = 0.39, p_{t+3} = 0.34, p_{t+4} = 0.26, p_{t+5} = 0.17$  with a continuous

decline in A support. Adding 3 more cycles would result in zero A support with  $p_{t+6} = 0.08$ ,  $p_{t+7} = 0.02$  and  $p_{t+8} = 0.00$ . Given any initial distribution of opinions, the random local opinion update leads toward a total polarisation of the collective opinion. Individual and collective opinions stabilise simultaneously along the same and unique vote intention either A or B.

The update cycle number to reach either one of the two stable attractors can be evaluated from Eq. (2.2). It depends on the distance of the initial densities from the unstable equilibrium. However, every update cycle takes some time length, which may correspond in real terms to some number of days. Therefore, in practical terms the required time to eventually complete the polarisation process is much larger than any public debate duration, thus preventing it to occur. Accordingly, associate elections never take place at the stable attractors. From the above example at  $p_t = 0.45$ , two cycles yield a result of 39% in favour of A and 61% in favour of B. One additional update cycle makes 34% in favour of A and 66% in favour of B.

We can now insert the existence of inflexibles. To grasp fully its social meaning we will introduce it in several steps. For the first one, inflexibles are present only on one side, say A. We thus have  $b = 0$  which yields  $a = x$ . Eq. (2.2) becomes

$$p_{t+1} = -2p_t^3 + p_t^2(3 + x) - 2xp_t + x. \quad (2.4)$$

Solving the associated fixed point equation  $p_{t+1} = p_t$  yields the three solutions

$$p_{B,a} = \frac{1}{4} \left( 1 + x - \sqrt{1 - 6x + x^2} \right), \quad (2.5)$$

$$p_c = \frac{1}{4} \left( 1 + x + \sqrt{1 - 6x + x^2} \right), \quad (2.6)$$

and  $p_A = 1$  to be compared to the bare results ( $x = 0$ )  $p_B = 0$ ,  $p_c = \frac{1}{2}$  and  $p_A = 1$ . While  $p_B$  and  $p_c$  have been shifted toward one another,  $p_A$  stayed unchanged as in the upper part of Fig. 2.2.

From above expressions an increase in  $x$  gets closer the attractor  $p_{B,a}$  and the separator  $p_c$  before they coalesce at  $x_c = 3 - 2\sqrt{2} \approx 0.17$ , and there disappear as seen in Fig. 2.5. The attractor  $p_A$  stays independent of  $x$ . Therefore for  $x > 0.17$  the unique fixed point of the dynamics is the attractor  $p_A = 1$ . Any initial support in A leads to its victory.

Fig. 2.6 shows the variation of  $p_{t+1}$  as a function of  $p_t$  for these two regimes. It is worth to note that in the second regime the dynamics of the winning inflexible minority is slowed down in some window of support before it starts to increase at a speedy path.

For instance  $p_t = 0.20$  leads successively to the series  $p_{t+1} = 0.23$ ,  $p_{t+2} = 0.25$ ,  $p_{t+3} = 0.27$ ,  $p_{t+4} = 0.29$ ,  $p_{t+5} = 0.30$ ,  $p_{t+6} = 0.32$ ,  $p_{t+7} = 0.33$ ,  $p_{t+8} = 0.34$ ,  $p_{t+9} = 0.36$ ,  $p_{t+10} = 0.38$ ,  $p_{t+11} = 0.40$ ,  $p_{t+12} = 0.42$ ,  $p_{t+13} = 0.45$ ,  $p_{t+14} = 0.49$ ,  $p_{t+15} = 0.53$ ,  $p_{t+16} = 0.59$ ,  $p_{t+17} = 0.67$ ,  $p_{t+18} = 0.77$ ,  $p_{t+19} = 0.87$ ,  $p_{t+20} = 0.96$ ,  $p_{t+21} = 1.00$ , with a continuous increase in A support. However 15 updates are

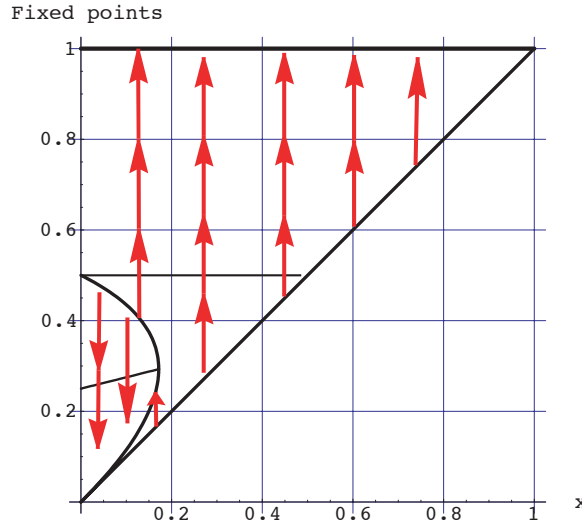


Figure 2.5: One sided inflexibles fixed points as a function of their density  $x$ . One line of attractors  $p_A = 1$ . In the regime  $x < 0.17$  the left upper part of the curved line is a line of separator (Eq. (2.5)) while the lower part is a line of attractor (Eq. (2.6)). Both are symmetrical with respect to the line  $\frac{1+x}{4}$  at which they eventually coalesce at  $x_c = 3 - 2\sqrt{2} \approx 0.17$ . The diagonal line delimits the floater region for A holders since  $p \geq x$ . As soon as  $x > 0.17$  the victory is granted for opinion A.

necessary for A to reach the majority from its initial 20%. Before, at  $x = 0$ , 8 updates were reducing a 45% support to zero while now 15 are required to gain 30%.

In terms of real time durations, a number of 15 updates may imply many months. Fig. 2.7 shows two initial supports  $p_t = 0.20$  and  $p_t = 0.52$  for respectively  $x = 0$  and  $x = 0.20$ . The differences in the associated dynamics are drastic.

We note that setting  $x = -b$  defines the symmetric situation with inflexibles only on side B. We then have  $a = 0$  and  $b$  for the respective densities of inflexibles. Above results then apply to the B opinion with the variable  $b$  playing the role of  $x$ .

At this point to have inflexibles on its side appears to be a decisive step towards leading the opinion competition. Accordingly both opinions are expected to have inflexibles. in case of a symmetric presence of inflexibles on both sides with  $x = 0$  and  $b \neq 0$ , i.e.,  $a = b \neq 0$ . In addition, since the total density of both side inflexibles is  $2b$ , the variable  $b$  must obeys  $b \leq \frac{1}{2}$ . Eq. (2.2) becomes

$$p_{t+1} = -2p_t^3 + 3p_t^2 - 2bp_t + b, \quad (2.7)$$

whose fixed points are

$$p_{B,a} = \frac{1}{2} \left( 1 - \sqrt{1 - 4b} \right), \quad (2.8)$$

$$p_{A,b} = \frac{1}{2} \left( 1 + \sqrt{1 - 4b} \right), \quad (2.9)$$

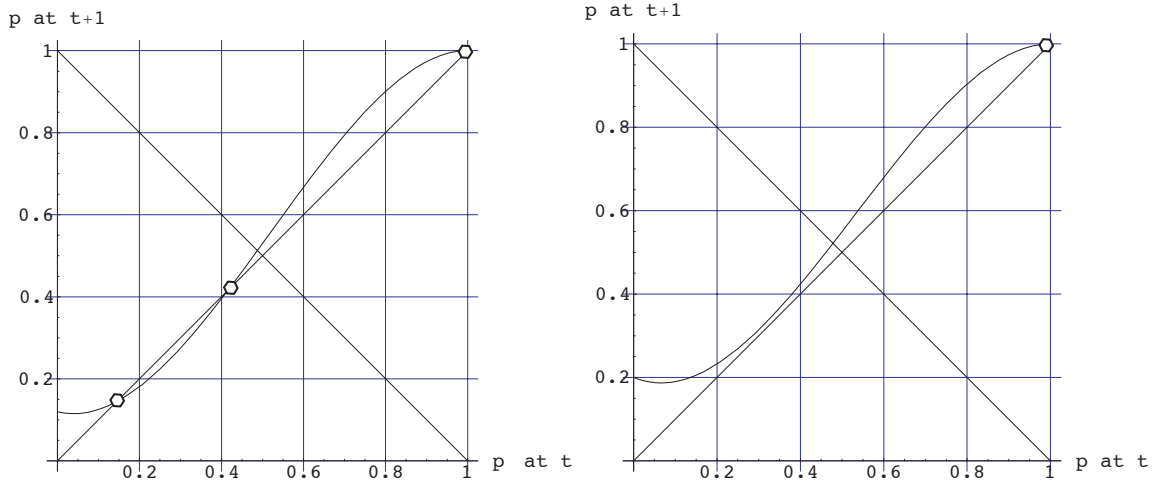


Figure 2.6: One sided inflexibles. The left part corresponds to  $x < 0.17$  of inflexibles in favour of opinion A. The right part shows the case of  $x > 0.17$ , which does grant the victory to opinion A.

and  $p_c = \frac{1}{2}$ . The symmetry restoring has put back the separator at  $\frac{1}{2}$  independently of  $b$ . The two mixed phase attractors  $p_{B,a}$  and  $p_{B,a}$  are now symmetric and move towards  $p_c$  as a function of increasing  $b$ . It is again the initial majority which wins the competition.

Nevertheless at  $a = b = \frac{1}{4}$  the dynamics is turned up side down with  $p_{B,a}$  and  $p_{A,b}$  merging at  $p_c = \frac{1}{2}$ , which at once becomes an attractor and the unique fixed point of the dynamics. Any initial condition leads to a hung equilibrium with an identical support of 50% for both opinions.

The topology of the fixed points as a function of the common density  $b$  of both side inflexibles is shown in Fig. 2.8. It is rather different from the one sided inflexibles of Fig. 2.5.

The variation of  $p_{t+1}$  as a function of  $p_t$  is shown in Fig. 2.9 for the two regimes  $b < \frac{1}{4}$  and  $b > \frac{1}{4}$ . It is worth to notice that the presence of contrarians leads to the same scenario [23]. However, the bare mechanism and its psycho-sociological meaning are quite different. In addition, while 17% of contrarians are necessary to reverse the dynamics,  $2 \times 25\% = 50\%$  of inflexibles are needed to accomplish the same reversal. A thorough study of the combined effect of simultaneous contrarians and inflexibles is under investigation [51]. Nevertheless, it is shown below that this similarity holds only for the case of equal densities of inflexibles for each opinion.

It is certainly realistic to consider inflexibles on both sides, but the symmetric hypothesis is peculiar. To account for the numerous situations, which exhibit different densities of inflexibles, we now study the effect of a discrepancy in  $a$  and  $b$ .

It is thus the general form of Eq. (2.2) which has to be solved to determine its associated fixed points. It yields the cubic equation

$$y_t^3 + Ay_t + B = 0, \tag{2.10}$$

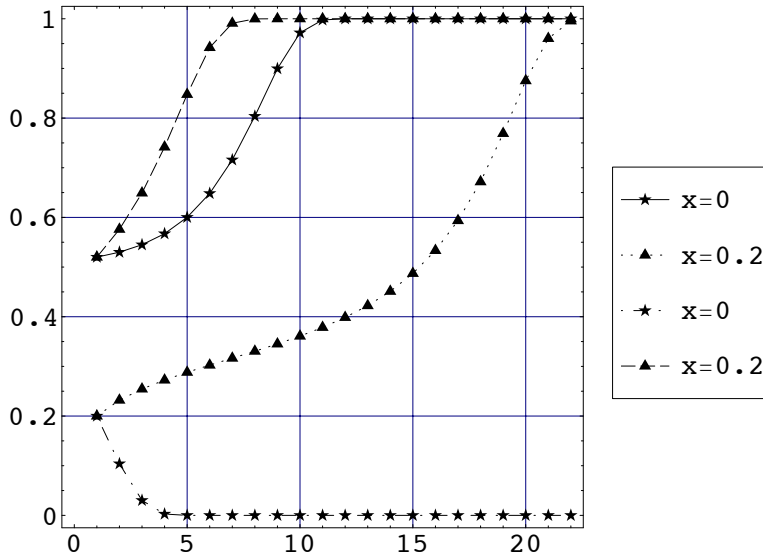


Figure 2.7: Comparison of the update series from two initial supports  $p_t = 0.52$  and  $p_t = 0.48$  for the pure floater case  $x = 0$  and one sided inflexible with a density  $x = 0.20$  above the threshold  $x_c \approx 0.17$ . In the latter case the victory is granted for opinion A although it starts from such a lower support of 20%. Nevertheless the process is rather slow.

which can be solved analytically with  $y_t \equiv p_t - \frac{3+x}{6}$ ,  $A \equiv \frac{1+2b+2x}{2} - \frac{(3+x)^2}{12}$  and  $B \equiv -\frac{b+x}{2} + \frac{(3+x)(1+2b+2x)}{12} - \frac{(3+x)^3}{108}$ . The solution depends on the sign of the discriminant

$$D = \frac{A^3}{27} + \frac{B^2}{4}. \quad (2.11)$$

Being interested in the nature of the associated dynamics what matters is the number of real roots. Their respective formulations being rather anaesthetic formulas in  $b$  and  $x$ , we do not explicit them. But we note that for  $D < 0$  there exists three distinct real solutions, for  $D = 0$  there are three real solutions of which at least two are equal, and for  $D > 0$  there are one single real root and two imaginary roots.

- (1) The first case of three real solutions ( $D < 0$ ) corresponds to the existence of a separator and two attractors as shown in the left part of Fig. 2.10. Any positive  $x$  (more inflexibles in favour of opinion A), shifts the separator below 50% as in the case of one sided inflexible. For instance  $b = 0.15$  and  $x = 0.02$  yield  $p_{B,a} = 0.22$ ,  $p_c = 0.47$  and  $p_{A,b} = 0.82$ . A 2% difference in inflexible produces a substantial unbalance of the democratic frame of the public debate since the A opinion needs to start with an initial support larger than 47% to be sure to win an associated election provided the campaign duration is long enough.

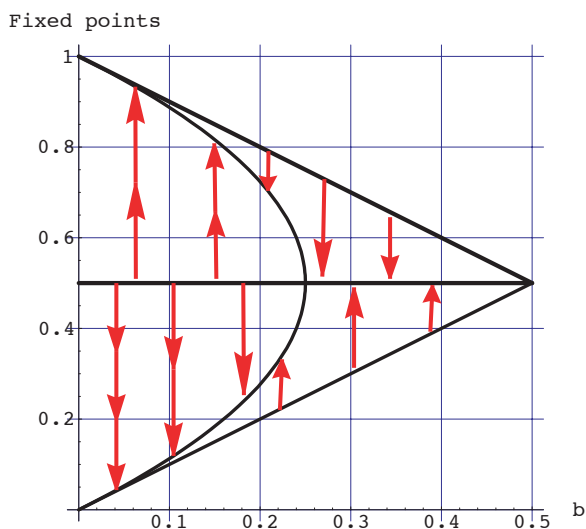


Figure 2.8: Two side symmetric inflexibles fixed points as a function of their density  $b$ . The first part of the line  $p_c = \frac{1}{2}$  till  $b = \frac{1}{4}$  is a separator. From there, it becomes the unique attractor of the dynamics. The left curved line is a line of mixed phase attractors  $p_{A,b}$  (upper part, Eq. (2.5)) and  $p_{B,a}$  (lower part, Eq. (2.6)). Both are symmetrical with respect to the line  $\frac{1}{2}$  at which they eventually coalesce at  $b_c = \frac{1}{4}$ . The two lines  $b$  and  $(1 - b)$  delimits the floater region for A holders since  $p \geq b$  with  $b \leq \frac{1}{2}$ . As soon as  $b > \frac{1}{4}$  no opinion wins.

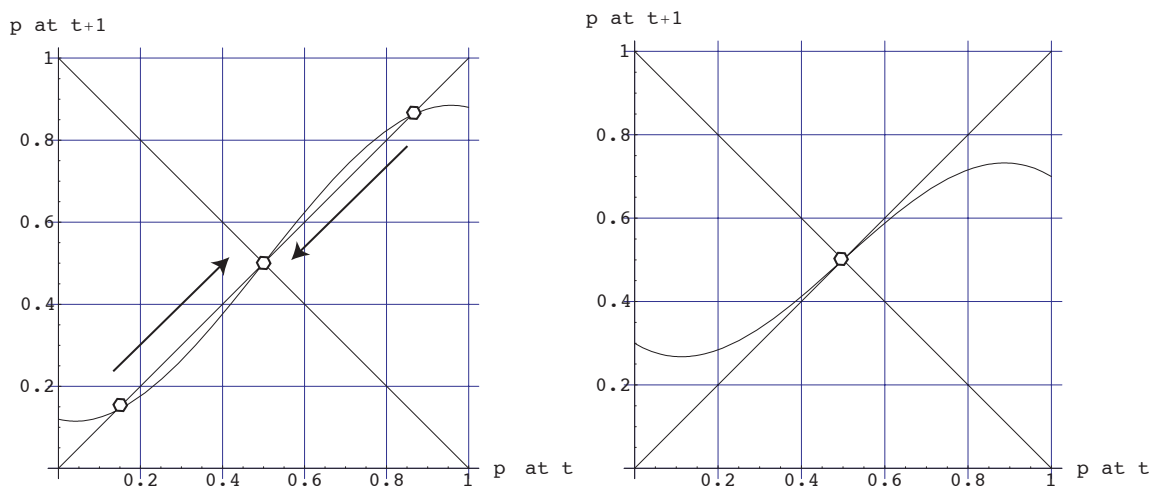


Figure 2.9: Two sided inflexibles. The left part corresponds to  $x = 0$  and  $b < 0.25$  of inflexibles for each of the two opinions. The two arrows along the diagonal show the directions in which the two attractors move when the equal densities of inflexibles are increased. The right part shows the case of  $x = 0$  and  $b > 0.25$ , which always yields a stable hung fifty-fifty equilibrium.

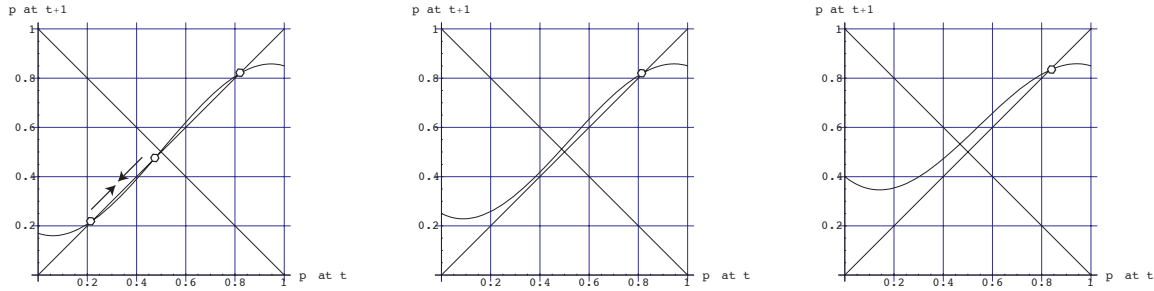


Figure 2.10: Two side asymmetric inflexibles. The left part corresponds to  $b = 0.15, x = 0.02$  with three fixed points  $p_{B,a} = 0.22$  (attractor),  $p_c = 0.47$  (separator) and  $p_{A,b} = 0.82$  (attractor). The two arrows along the diagonal show the directions in which the two attractors move when the difference  $x$  in densities of inflexibles is increased. In the middle part  $b = 0.15$  and  $x = 0.10 > x_c = 0.055$  putting the dynamics in the case with the single fixed point  $p_{A,b}$  (attractor). The flow is very slow. The right part shows a larger value  $x = 0.15$  with still  $b = 0.15$ , which accelerates the converging towards the unique attractor of the dynamics.

For instance, an initial  $p_t = 0.48$  leads to the series  $p_{t+1} = 0.481, p_{t+2} = 0.483, p_{t+3} = 0.485, p_{t+4} = 0.487, p_{t+5} = 0.490, p_{t+6} = 0.493, p_{t+7} = 0.497$  and  $p_{t+8} = 0.502$ . Eight updates are necessary to cross the winning bar of fifty percent, i.e. to gain 2.2%. To reach a higher score requires more updates with the follow up of  $p_{t+9} = 0.507, p_{t+10} = 0.513, p_{t+11} = 0.521, p_{t+12} = 0.529, p_{t+13} = 0.539, p_{t+14} = 0.551, p_{t+15} = 0.566, p_{t+16} = 0.582, p_{t+17} = 0.601$ . Nine additional updates makes the support in favour of A to exceed sixty percent. The majority reversal is here much slower than in the precedent cases.

It is worth to emphasise that the initial value  $p_t = 0.46 < p_c$  leads to the victory of the B opinion since it starts below the separator located at  $p_c = 0.47$ . By symmetry, a negative value  $x = -0.02$  with the initial value  $p_t = 0.52$  yields the advantage to opinion B which wins the majority with the same above dynamics.

- (II) Furthermore, given  $b$  and increasing  $x > 0$  results in a continuous shrinking of the distance between the separator  $p_c$  and the mixed phase attractor  $p_{B,a}$ . At some threshold value  $x_c$  both fixed points coalesce. We are then in the second case with two real solutions whose one is double ( $D = 0$ ). At reverse, for  $x < 0$  it is  $p_c$  and  $p_{A,b}$  which coalesce at  $x = -x_c$ . Above choice  $b = 0.15$  yields  $x_c = 0.055$ .
- (III) Afterwards for  $x > x_c$  the two fixed points which have coalesced disappear leaving  $p_{A,b}$  as the single attractor of the dynamics. To disappear means

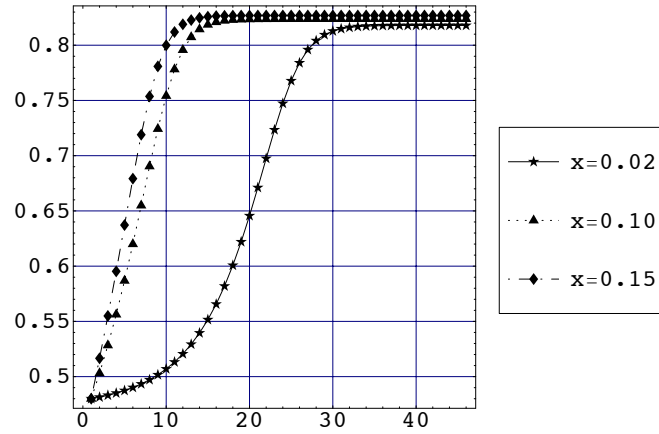


Figure 2.11: Evolution of an initial A support  $p_t = 0.48$  (ordinate) as a function of repeated updates whose number is put on the abscis. Three different series are shown for respectively  $x = 0.02, 0.10, 0.15$  with  $b = 0.15$ . The two extreme cases  $x = 0.02$  and  $x = 0.15$  yields a similar dynamics. However in the first case an initial  $p_t = 0.46$  would lead the the B victory at contrast with the second case where A wins always.

they became imaginary, we are in the third case  $D > 0$  with one single real solution  $p_{A,b}$ .

For  $x > x_c$ , in the vicinity of  $x_c$  the flow is very slow as seen in the middle part of Fig. 2.10 where we have the set  $(b = 0.15, x = 0.10)$ . The dynamics in the third case with only one unique fixed point, an attractor and above initial value  $p_t = 0.48$  yields now the series  $p_{t+1} = 0.503$ ,  $p_{t+2} = 0.528$ ,  $p_{t+3} = 0.556$ ,  $p_{t+4} = 0.587$ ,  $p_{t+5} = 0.620$ .

One single update is now sufficient to rise the minority opinion A to the status of majority as compared to eight updates above. Only four additional updates reach the sixty percent bar instead of the previous nine. The majority reversal has been accelerated.

Going to the set  $(b = 0.15, x = 0.15)$  makes the dynamics faster as exhibited in the right part of Fig. 2.10. We now have from  $p_t = 0.48$  the series  $p_{t+1} = 0.517$ ,  $p_{t+2} = 0.555$ ,  $p_{t+3} = 0.595$ ,  $p_{t+4} = 0.637$ ,  $p_{t+5} = 0.679$ .

As soon as  $\pm x_c$  are reached the dynamics ineluctably leads the opinion which have the surplus of inflexibles to invade the majority of the population (A for  $x_c$  and B when  $\pm x_c$ ). The above three different series for  $b = 0.15$  and  $x = 0.02, 0.10, 0.15$  are reproduced in Fig. 2.11.

It thus appear to be of a central importance to determine the value of  $x_c$  given the value of  $b$ . Once the associated opinion reached a surplus of inflexibles  $x_c$  it eventually wins the election with certainty. To achieve this goal, we need to solve



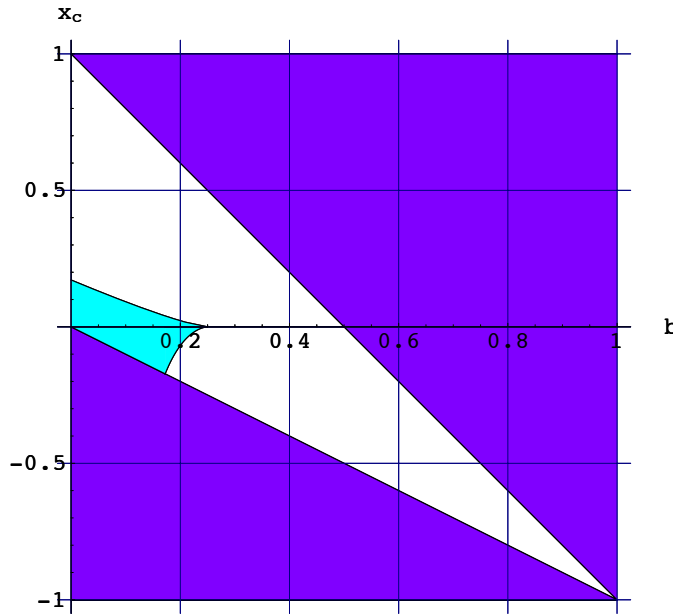


Figure 2.12: The dynamics map. The white triangle delimited by  $0 \leq b \leq 1$  and  $-b \leq x \leq 1 - 2b$  shows the accessible range for the respective values of  $b$  and  $x$ . Within the accessible area, the left aqua-coloured area corresponds to region where  $D < 0$ , and the dynamics is monitored by a separator and two attractors with  $x_{c2} < x < x_{c1}$  where  $x_{c2} \leq 0$  and  $x_{c1} \geq 0$ . Outside this closed area, the dynamics is driven by a single attractor.

the equation  $D = 0$  as a function of the variable  $x$ ,  $b$  being a fixed parameter, where  $D$  is given by Eq. (2.11).

Performing a Taylor expansion of Eq. (2.11) in power of  $x$  at order 2 leads to the solutions

$$x_{c1,c2} = \frac{3 - 24b + 48b^2 \mp 2(-1 + 4b)^{3/2}\sqrt{-2 + b + b^2}}{1 - 32b + 4b^2}, \quad (2.12)$$

which are shown in Fig. 2.12 together with the available values for  $(b, x)$  constrained by the frontiers  $0 \leq b \leq 1$  and  $-b \leq x \leq 1 - 2b$ . The positive value  $x_{c1}$  exists for the range  $0 \leq b \leq \frac{1}{4}$ , while for the negative value  $x_{c2}$  it is the range  $3 - 2\sqrt{2} \approx 0.17 \leq b \leq \frac{1}{4}$ .

In the region  $x_{c2} < x < x_{c1}$ ,  $D < 0$  which yields a separator and two attractors. At odd, outside this closed area and with  $-b < x < 1 - 2b$ , we have  $D < 0$  with one single attractor. The case  $x > 0$  guarantees the A victory while  $x < 0$  grants the B victory. The various domains are shown in Fig. 2.12. It appears that  $D > 0$  for  $b > \frac{1}{4}$ . A positive  $x$  yields a A victory while a negative  $x$  a B victory. The three fixed points coalesce at the unique set  $b = \frac{1}{4}, x = 0$ .

### 2.3 CONCLUSIONS

We have singled out the effect of inflexible choices on the democratic opinion forming. An inflexible being an agent who always sticks to its opinion without any shift. At low and equal densities, they prevent the trend towards a total polarisation of floaters along one unique opinion. The opinion dynamics is found to lead to a mixed phase attractor with a clear cut majority-minority splitting. Below 25% of equal density inflexibles for both opinions, the initial majority opinion wins the public debate. At contrast, beyond 25% the dynamics is reversed and converge towards a fifty-fifty attractor. Therefore an equal density of inflexibles produces effects which can also be achieved by sufficiently low densities of contrarians [23].

However, even a very small asymmetry in the respective inflexibles densities upsets the balanced character of above results. At a very low difference, the main effect is to shift the separator from fifty percent to a lower value at the advantage of the larger inflexible opinion. It also increases its incompressible minority support. Moreover, an excess in inflexibles beyond some small threshold  $x_c$ , which depends on  $b$ , grants the victory to the beneficiary opinion. In this regime there exists only one single attractor, which drives the corresponding opinion to an overwhelming majority. Nevertheless it is worth to emphasise that the associated dynamics may become rather slow.

Fig. 2.12 sums up our results. It allows to determine which strategy is best for a given opinion to win the public debate competition. It appears that the decisive goal should be to get a lead, even small, in the respective inflexible densities. It immediately produces the substantial advantage to lower the separator from 50%. A larger difference in inflexibles, whose amplitude varies as a function of the other opinion support, guarantees the winning of the campaign, and eventually the follow up election.

On this basis we plan to extend our study to larger size update groups. We also plan to combine both effects of contrarians and inflexibles to study the dynamics of floaters [51].

## TWO-OPINIONS-DYNAMICS GENERATED BY INFLEXIBLES AND NON-CONTRARIAN AND CONTRARIAN FLOATERS

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This chapter is based on:

F. Jacobs and S. Galam, Two-opinion-dynamics generated by inflexibles and non-contrarian and contrarian floaters, *Advances in Complex Systems*, Volume 22 No. 04, 1950008, 2019

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### ABSTRACT

We assume a community whose members adopt one of two opinions  $A$  or  $B$ . Each member appears as an inflexible, or as a non-contrarian or contrarian floater. An inflexible sticks to its opinion, whereas a floater may change into a floater of the alternative opinion. The occurrence of this change is governed by the local majority rule: members meet in groups of a fixed size, and a floater then changes its opinion provided it is a minority in the group. Subsequently, a non-contrarian floater keeps the opinion as adopted under the local majority rule, whereas a contrarian floater adopts the alternative opinion. Whereas the effects of on the one hand inflexibles and on the other hand non-contrarians and contrarians have previously been studied separately, the current approach allows us to gain insight in the effect of their combined presence in a community. Given fixed proportions of inflexibles  $(\alpha_A, \alpha_B)$  for the two opinions, and fixed fractions of contrarians  $(\gamma_A, \gamma_B)$  among the  $A$  and  $B$  floaters, we derive the update equation  $p_{t+1}$  for the overall support for opinion  $A$  at time  $t + 1$ , given  $p_t$ . The update equation is derived respectively for local group sizes 1, 2 and 3. The associated dynamics generated by repeated local updates is then determined to identify its asymptotic steady configuration. The full opinion flow diagram is thus obtained, showing conditions in terms of the parameters for each opinion to eventually win the competing dynamics. Various dynamical scenarios are thus exhibited, and it is derived that relatively small densities of inflexibles allow for more variation in the

qualitative outcome of the dynamics than higher densities of inflexibles.

Keywords: Sociomathematics, sociophysics, opinion dynamics, local majority rule, contrarian behaviour, floating behaviour

PACS Classification: 05.70.Jk; 89.65.Cd; 89.65.Ef

### 3.1 INTRODUCTION

Within the growing field of sociophysics (see [31] for the defining paper and [30], [80], [88] for an impression of the state of the art), a great deal of work has been devoted to opinion dynamics [10]. The seminal Galam models of opinion dynamics [21, 24] and their unification [26] play a guiding role in analysing the process of opinion spreading in communities and in providing possible explanations for the outcome of elections. These models are centred around the *local majority rule* (l.m.r.), which is applied either in a deterministic or a probabilistic way. In the basic *deterministic* case, supporters of the two opinions present in a community are randomly distributed over groups of a fixed size  $L$ . Within each group members adopt the opinion that has the majority in that group, after which all group members are recollected again. In case there is no majority in a group, its members stick to their own opinion (i.e., *neutral* treatment; the *probabilistic* treatment in case of a tie assigns opinions to the group members according to a certain probability distribution). Repeated application of this principle generates what is called *randomly localised dynamics with a local majority rule*. In the basic *probabilistic* case, the community members are divided among groups of various sizes according to some probability distribution, and within each group all members adopt one of the possible opinions with either certainty (majority rule) or probability (at a tie in even-sized groups) [21].

In the basic deterministic two states opinion model, fast dynamics occurs in which the opinion that originally has the majority eventually will obtain complete presence at the cost of the alternative opinion. In the probabilistic two states opinion model, the final outcome depends on the probability distributions for group sizes and local adaptation. Eventually the state of the community can be

either one in which only the opinion with initial majority or minority remains, or one with a perfect consensus on both opinions (see [26], which unifies basic probabilistic two states opinion models).

In [37] a three states opinion model is introduced in which the community members are randomly distributed over groups of size 3. Within each group the l.m.r. is applied, with the additional rule that in case of a tie all members of the group adopt one of the three opinions according to some probability distribution. It is shown that the dynamics quickly converges to a state in which only one of the three opinions is present, which may be an opinion that initially has a minor presence in the community. In addition, the effect of non-voting persons (abstention, sickness, apathy) was shown to have drastic effect on the asymmetry of the threshold value to power [33].

As a next step to gain a better insight into opinion dynamics, in [23] the basic deterministic two states Galam opinion model is extended by the introduction of so-called contrarians. A *contrarian* is a community member who, instead of keeping the opinion it adopted under the l.m.r., switches to the alternative opinion. Contrarian behaviour can manifest itself in various ways, e.g. in adolescents as a strive for individualisation, especially in an environment of inflexible opinion supporters (see below), as an expression of conformity with the minority, and as negative voting in order to diminish the support for a majority. Depending on the density<sup>1</sup> of contrarians as well as on group size, their presence either leads to a stabilisation of the opinion dynamics in which one opinion (the one with the lower density of contrarians) dominates the other, to an equilibrium in which neither opinion dominates (in case both opinions have equal densities of contrarians), or (in case of relatively large densities of contrarians for both opinions) to a dynamics in which the dominating opinion constantly alternates between the two opinions. The incorporation of contrarians in opinion dynamics models was a step towards a possible explanation of the “hung elections” outcome in the U.S. presidential elections in 2000. Although introducing contrarians to explain “hung elections” at the time may have been a bit speculative (and being

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<sup>1</sup> All opinion dynamics models considered in this article are understood to refer to large communities and sub-communities (e.g. contrarians) in which the size of a sub-community can effectively be described by its density (the part of the sub-community’s size with respect to the whole community) instead of by discrete whole numbers.

aware that possible other influences such as finite population sizes and exogenous factors influencing opinion dynamics have not been considered), it was concluded that if the assumption was sound, under similar conditions the phenomenon should repeat itself in the following years in democratic countries. And indeed, ‘hung elections’ occurred again several times as with the German elections in 2002 and 2005 as well as the 2006 Italian elections [28]. The origin of contrarian behaviour as well as its implications have been the focus of numerous studies [7, 12, 20, 36, 65–67, 76–78, 87, 93, 95, 97, 100, 101].

In addition to the incorporation of contrarian behaviour, the basic deterministic two states Galam model has been modified introducing opinion supporters that express what in politics (and other games) is called *inflexible behaviour* [32, 34]. An inflexible community member is a supporter that under all conditions sticks to its opinion. Under this terminology supporters that switch opinion when in the minority then classify as *floaters*, and we shall use this distinction in what follows. In [34] the effect of inflexible behaviour on opinion dynamics is studied for the case that opinion supporters repeatedly meet in groups of fixed size 3. It is shown that a small density of inflexibles for only one of the two opinions allows for the existence of two local attractors. One of these local attractors is a mixed one, on which both opinions are present and on which the opinion that is supported by inflexibles is a minority. The other attractor is a single state attractor, on which the opinion that is supported by inflexibles has complete majority, i.e., its density equals 1, the other opinion being absent. Due to the presence of these two attractors, the outcome of the opinion dynamics thus depends on the initial condition, the basin of attraction for the mixed local attractor being relatively small compared to that for the single state attractor. If the density of inflexibles is sufficiently large (approximately 17%), the mixed attractor disappears and the single state attractor becomes global. In case both opinions have small and equal densities of inflexibles there are two mixed local attractors. These two attractors are symmetrically situated with regard to a separator on which both opinions are present with density 0.5.

A change in the density of inflexibles for one of the opinions breaks this symmetry, and a sufficiently large increase may lead to a global attractor on which the opinion with the larger density of inflexibles has the majority [34]. The inflexible effect could provide for some counter-intuitive explanation to real paradoxical situations

[29]. The effect of inflexibles and floaters on opinion dynamics has also been studied extensively in recent years, as seen in [3, 5, 9, 42, 55, 63, 64, 74, 81–83, 90]. In this paper we combine the approaches presented in [23] and [34], by allowing for groups composed of inflexibles as well as contrarian and non-contrarian opinion supporters. For clarity we restrict ourselves to groups of fixed size 1, 2 and 3. For both opinions we assume fixed densities for the inflexibles. Also, we consider the contrarians to be part of the floaters, i.e., in a given group the contrarians first determine their opinion according to the l.m.r., and subsequently change to become a floater (not necessarily a contrarian) for the alternative opinion (which thus may be the opinion that the contrarian initially was supporting). The presence of contrarians for each opinion is quantitatively expressed as a fixed fraction of the density of floaters of the respective opinion. In case of a tie in groups of size 2 we apply the neutral treatment. After an opinion update, all supporters for both opinions are recollected and then are redistributed again, either as an inflexible or as a non-contrarian or contrarian floater, according to the fixed densities for inflexibles and the fixed fractions of contrarians for the two opinions. We study qualitative characteristics of the opinion dynamics generated by repeated updates. In particular we study changes in the number of equilibria, and changes from monotone to alternating dynamics, due to changes in parameter combinations. The opinion dynamics thus obtained reflects the behaviour of the support for opinions as it is influenced by individuals that for various (e.g. psychological, political) reasons go against the grain as they find themselves in a background consisting of individuals with a clear conviction. A detailed mathematical extension to groups of size 4 will be given in a forthcoming paper [35].

### *Notation*

We denote the two opinions by  $A$  and  $B$ . The densities of inflexibles for the  $A$  and  $B$  opinion are denoted by  $\alpha_A$  and  $\alpha_B$  respectively, with  $0 \leq \alpha_A \leq 1$  as well as  $0 \leq \alpha_B \leq 1$ , and in addition  $0 \leq \alpha_A + \alpha_B \leq 1$ . Since the roles of the  $A$  and  $B$  opinion are interchangeable in deriving the opinion dynamics, we may without loss of generality assume that  $0 \leq \alpha_A \leq 0.5$ , and we shall do so in what follows.

The fraction of contrarians among the  $A$  floaters is denoted by  $\gamma_A$ , and  $\gamma_B$  denotes the fraction of contrarians among the  $B$  floaters, with both  $0 \leq \gamma_A \leq 1$  and  $0 \leq \gamma_B \leq 1$ . The size of the groups in which opinion supporters meet is denoted by  $L$ . The density of the  $A$  opinion at time  $t = 0, 1, 2, \dots$  (or after  $t$  updates) shall be denoted as  $p_t$ . Note that for given  $\alpha_A$  and  $\alpha_B$  the density  $p_t$  necessarily lies in the interval  $[\alpha_A, 1 - \alpha_B]$  (independent of  $L$ ,  $\gamma_A$  or  $\gamma_B$ ). With  $f_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  we denote the function that determines the density of the  $A$  opinion after application of the l.m.r. followed by the switch of the contrarians. Thus,  $p_{t+1} = f_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p_t)$ . Setting  $\gamma_A = \gamma_B = 0$ ,  $p_{t+1} = f_{L;\alpha_A,\alpha_B;0,0}(p_t)$  then gives the density obtained from  $p_t$  when the l.m.r. is applied without being followed by the switch of the contrarians. In the Appendix tables are given, presenting all possible group compositions in terms of inflexibles and non-contrarian and contrarian floaters for group sizes  $L = 1$  to  $3$ , together with the effects of the l.m.r. and the opinion changes of contrarians. It is assumed that the community is sufficiently large and well-mixed to allow for the derivation of the density of each possible group composition in the ensemble of all groups of a fixed size from the densities in the community of the constituents of a group. From these tables the expressions for  $f_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  are obtained.

With  $\overrightarrow{f_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$  we denote the dynamics generated by repeated application of  $f_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  in subsequent timesteps. Furthermore,  $\hat{p}_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  denotes an asymptotically stable equilibrium for  $\overrightarrow{f_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$  and  $p_{L;\alpha_A,\alpha_B;\gamma_A,\gamma_B}^*$  refers to an asymptotically stable periodic point.

We now turn to the treatment of the opinion dynamics for group sizes  $L = 1, 2$  and  $3$ .

### 3.2 GROUP SIZE 1

The case  $L = 1$  resembles a community in which each member is unaffected by other community members in determining its opinion, and the only changes in opinion come from the contrarians. The contributions to the  $A$  density after application of the local majority rule is obtained from the second column in Table 1 in Appendix 3.6.1. This column obviously is equal to the first one, since in groups



of size 1 local majority is automatically obtained, but is without effect on the opinion densities. These contributions are:  $\alpha_A$  for the  $A$  inflexibles, and  $p - \alpha_A$  for the (non-contrarian and contrarian)  $A$  floaters. Their sum is  $p$ , and we obtain for the update rule of the local majority rule that

$$p_{t+1} = f_{1;\alpha_A,\alpha_B;0,0}(p_t) = p_t; \quad (3.1)$$

consequently, each  $p \in [\alpha_A, 1 - \alpha_B]$  is a neutrally stable equilibrium for the opinion dynamics generated by the l.m.r.

In case only (non-contrarian and contrarian) floaters are involved both  $\alpha_A$  and  $\alpha_B$  are equal to 0, and we restrict ourselves to the contributions from the second, third, fifth and sixth line in the table. Since the l.m.r. leaves each group of size 1 unaffected, a switch by a contrarian in this case necessarily implies a change to the opinion it initially does not support. Thus, here also a contribution to the  $A$  density comes from the group that initially consists of only  $B$  contrarians, as these will turn into  $A$  floaters. In this case we obtain for the contribution to the  $A$  density:

$$p_{t+1} = f_{1;0,0;\gamma_A,\gamma_B}(p_t) = (1 - \gamma_A)p_t + \gamma_B(1 - p_t) = \gamma_B + (1 - (\gamma_A + \gamma_B))p_t. \quad (3.2)$$

The effect of both inflexibles and non-contrarian as well as contrarian floaters is obtained by adding all the expressions in the last column: the contributions  $\alpha_A$  due to the invariant density of  $A$  inflexibles,  $(1 - \gamma_A)(p_t - \alpha_A)$  from the non-contrarian  $A$  floaters, and  $\gamma_B(1 - \alpha_B - p_t)$  from the contrarian  $B$  floaters. This yields:

$$p_{t+1} = f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p_t) = \alpha_A + (1 - \gamma_A)(p_t - \alpha_A) + \gamma_B(1 - \alpha_B - p_t) = \\ \alpha_A\gamma_A + (1 - \alpha_B)\gamma_B + (1 - (\gamma_A + \gamma_B))p_t. \quad (3.3)$$

It follows that if  $\gamma_A + \gamma_B > 0$ , then

$$\hat{p} = \frac{\alpha_A\gamma_A + (1 - \alpha_B)\gamma_B}{\gamma_A + \gamma_B} \quad (3.4)$$

is the unique equilibrium for the opinion dynamics  $\xrightarrow{f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$ . Due to its linearity as a function of  $p_t$ , expression (3.3) implies that the dynamical characteristics of this equilibrium are governed solely by the frequencies of the contrarians.

The equilibrium is asymptotically stable if and only if  $0 < \gamma_A + \gamma_B < 2$ . For  $0 < \gamma_A + \gamma_B < 1$  the equilibrium is approached monotonically, with an increase in the  $A$  density if and only if its initial value is less than the equilibrium value. For  $\gamma_A + \gamma_B = 1$ , the function  $f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  is constant and equals  $\alpha_A\gamma_A + (1 - \alpha_B)\gamma_B$ ; the opinion dynamics then reaches its equilibrium in one iteration. For  $1 < \gamma_A + \gamma_B < 2$ , the equilibrium is approached alternately. For  $\gamma_A + \gamma_B = 2$ , i.e., both  $\gamma_A = 1$  and  $\gamma_B = 1$ , the equilibrium equals  $0.5(1 + \alpha_A - \alpha_B)$  and is neutrally stable; each  $p \in [\alpha_A, 1 - \alpha_B]$  different from  $0.5(1 + \alpha_A - \alpha_B)$  generates a neutrally stable cycle of length 2.

On the equilibrium, the  $A$  opinion has the majority if and only if the inequality

$$(0.5 - \alpha_A)\gamma_A < (0.5 - \alpha_B)\gamma_B \quad (3.5)$$

holds. Thus, for an opinion to achieve the majority it is required that it is being supported by a sufficiently large density of inflexibles, and/or a sufficiently small frequency of contrarians among the floaters.

Given densities  $\alpha_A$  and  $\alpha_B$  of inflexibles for the two opinions, a change in the frequencies of contrarians from 0 into small values  $\gamma_A$  and  $\gamma_B$  causes the bifurcation from a collection of neutrally stable equilibria for  $\overrightarrow{f_{1;\alpha_A,\alpha_B;0,0}}$  into a unique stable equilibrium for  $\overrightarrow{f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$ . The opinion which has the majority on this equilibrium is determined by inequality (3.5). In case  $\alpha_A = \alpha_B = \alpha$ , the opinion with the smaller frequency of contrarians obtains the majority. Conversely, given different frequencies  $\gamma_A$  and  $\gamma_B$  of contrarian floaters for the two opinions, in the absence of inflexibles the dynamics  $\overrightarrow{f_{1;0,0;\gamma_A,\gamma_B}}$  has  $\hat{p} = \frac{\gamma_B}{\gamma_A + \gamma_B}$  as its unique stable equilibrium, on which the opinion with the smaller frequency of contrarians has the majority. Fixing sufficiently small densities  $\alpha_A$  and  $\alpha_B$  of both opinions as inflexibles, this equilibrium slightly shifts but leaves the majority unaltered. In case  $\gamma_A = \gamma_B$ , in the absence of inflexibles the equilibrium  $\hat{p}$  equals 0.5, and the introduction of small densities of inflexibles for both opinions changes this equilibrium into one on which the opinion with the larger density of inflexibles takes the majority. Figure 3.1 illustrates these conclusions.

Figure 3.2 gives a qualitative overview of the outcomes of the possible opinion dynamics  $\overrightarrow{f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$ .

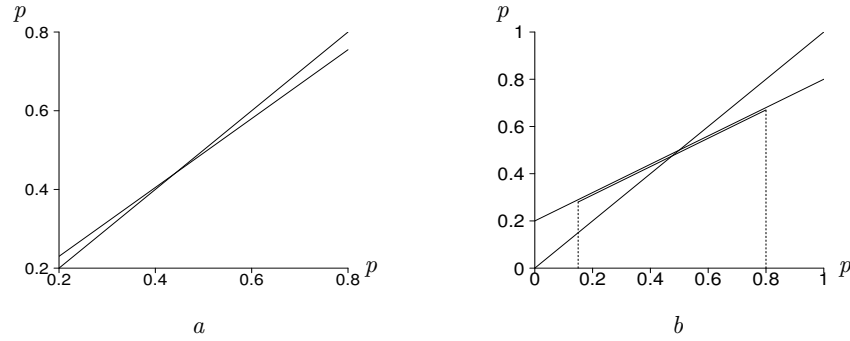


Figure 3.1: Figure *a* shows the graphs of  $f_{1;0.2,0.2;0,0}$  (which coincides with the diagonal) and  $f_{1;0.2,0.2;0.075,0.05}$  as functions of  $p$  on the interval  $[0.2, 0.8]$ . By changing the frequencies of contrarians from  $(\gamma_A, \gamma_B) = (0, 0)$  into  $(\gamma_A, \gamma_B) = (0.075, 0.05)$ , the collection of neutrally stable equilibria (the diagonal) bifurcates into a unique stable equilibrium  $\hat{p} = 0.44$  on which the *B* opinion has the majority. Figure *b* shows the diagonal together with the graph of  $f_{1;0,0;0.2,0.2}$  on  $[0, 1]$ , and the graph of  $f_{1;0.15,0.2;0.2,0.2}$  on  $[0.15, 0.8]$ , both as functions of  $p$ . The dashed lines indicate the boundaries of the interval  $[0.15, 0.8]$ . The graphs of the two functions almost coincide on this interval and are parallel (due to the equal frequencies of contrarians for both cases). The dynamics generated by these two functions have  $\hat{p} = 0.5$  and  $\hat{p} = 0.475$  as their respective stable equilibria.

### 3.3 GROUP SIZE 2

In groups of size 2 the number of members that support the *A* or *B* opinion may be equal, in which case a tie occurs. We shall deal with the neural treatment in case of a tie, in which each supporter keeps its own opinion.

Table 2 in Appendix 3.6.2 is related to groups of size 2. We obtain

$$p_{t+1} = f_{2;\alpha_A,\alpha_B;0,0}(p_t) = p_t, \quad (3.6)$$

which is obvious, since in groups of size 2 no majorities can occur, and, in case of a tie, the neutral application of the local majority rule does not have any effect. Incorporating the effect of non-contrarian as well as contrarian floaters, Table 2 yields that

$$p_{t+1} = f_{2;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p_t) = \alpha_A\gamma_A + (1 - \alpha_B)\gamma_B + \left(1 - (\gamma_A + \gamma_B)\right)p_t. \quad (3.7)$$

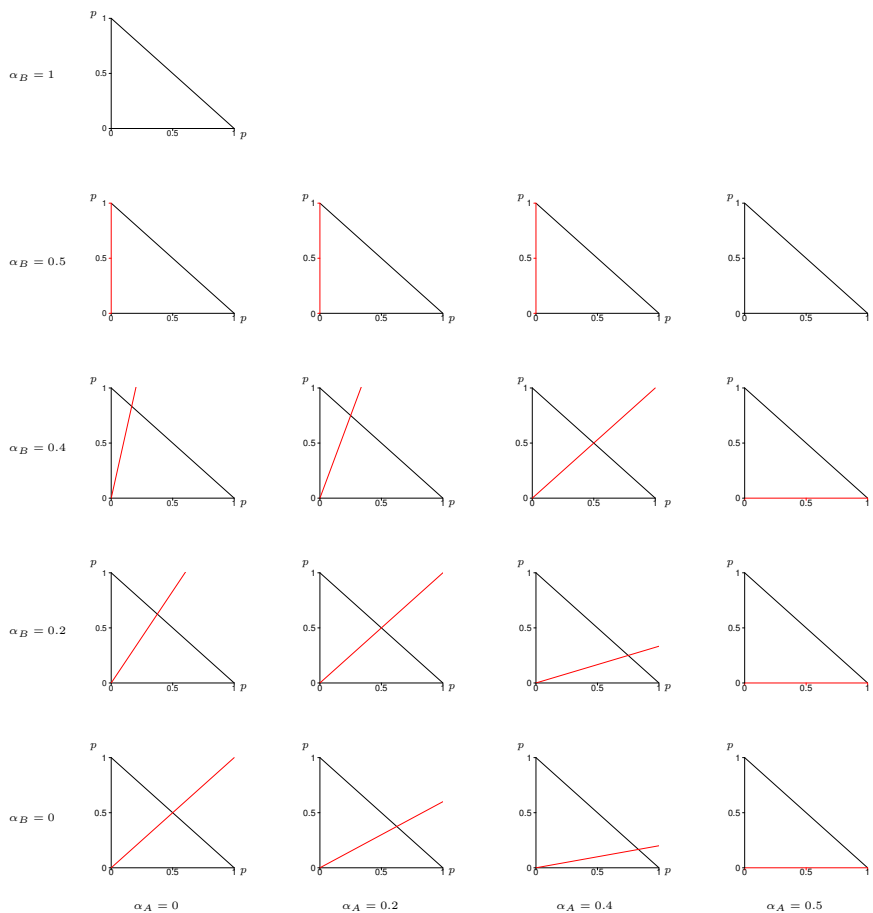


Figure 3.2: An overview of the opinion dynamics of  $f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  for values  $\alpha_A$  and  $\alpha_B$  as indicated, and with  $\gamma_A$  and  $\gamma_B$  in each pane on the horizontal and vertical axis, respectively, both ranging between 0 and 1. In each pane the line with negative slope  $\gamma_A + \gamma_B = 1$  is drawn, and possibly an additional red line of positive (possibly infinite) or zero slope. On the line  $\gamma_A + \gamma_B = 1$  the function  $f_{1;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  is constant, and the corresponding values of  $\gamma_A$  and  $\gamma_B$  separate between monotone and alternating dynamics, with the monotone dynamics occurring if  $0 < \gamma_A + \gamma_B < 1$ , i.e., below the line. The red line, if present, gives the values  $(\gamma_1, \gamma_2) \neq (0, 0)$  for which the equilibrium of the opinion dynamics equals 0.5, and is determined by the expression  $(\alpha_A - 0.5)\gamma_A - (\alpha_B - 0.5)\gamma_B = 0$ . Opinion A obtains the majority if (and only if)  $(\alpha_A - 0.5)\gamma_A - (\alpha_B - 0.5)\gamma_B > 0$  holds, i.e., if  $\alpha_B < 0.5$  and  $(\gamma_A, \gamma_B)$  lies above the red line. The panes for values  $(\alpha_A, \alpha_B)$  for which  $\alpha_A + \alpha_B = 1$  represent degenerate cases, in the sense that only inflexibles for both opinions are present in the community and only one density  $\hat{p} = \alpha_A$  for the A opinion occurs in time. In case  $\alpha_B > 0.5$ , opinion A will never achieve the majority in equilibrium.

Thus, for groups of size 2 the effect of the neutral application of the local majority rule and the contrarians is the same as for groups of size 1.

### 3.4 GROUP SIZE 3

Group size 3 is the smallest value of  $L$  for which the local majority rule becomes effective due to possible group compositions in which a majority of one of the two opinions occurs. As a consequence, the generated dynamics allows for features different from those for group sizes 1 and 2. Careful bookkeeping based on Table 3 in Appendix 3.6.3 yields that

$$\begin{aligned}
 p_{t+1} &= f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p_t) = \\
 &\alpha_A(1 - \gamma_A) + (1 - \alpha_B)\gamma_B - \left(2\alpha_A(1 - 2\gamma_A) - \gamma_A + \gamma_B\right)p_t + \\
 &\left(3 + \alpha_A(1 - 2\gamma_A) - \alpha_B(1 - 2\gamma_B) - 4\gamma_A - 2\gamma_B\right)p_t^2 - 2\left(1 - \gamma_A - \gamma_B\right)p_t^3 = \\
 &p_t + \alpha_A(1 - \gamma_A) + (1 - \alpha_B)\gamma_B - \left(1 + 2\alpha_A(1 - 2\gamma_A) - \gamma_A + \gamma_B\right)p_t + \\
 &\left(3 + \alpha_A(1 - 2\gamma_A) - \alpha_B(1 - 2\gamma_B) - 4\gamma_A - 2\gamma_B\right)p_t^2 - 2\left(1 - \gamma_A - \gamma_B\right)p_t^3. \quad (3.8)
 \end{aligned}$$

For clarity we start the analysis of the generated opinion dynamics with the symmetric case of equal densities of inflexibles and equal fractions of contrarians for both opinions.

#### 3.4.1 The fully symmetric case: $\alpha_A = \alpha_B$ and $\gamma_A = \gamma_B$

Taking  $\alpha_A = \alpha_B = \alpha$  and  $\gamma_A = \gamma_B = \gamma$ , we obtain that

$$\begin{aligned}
 p_{t+1} &= f_{3;\alpha,\alpha;\gamma,\gamma}(p_t) = \\
 &p_t + (1 - 2p_t)\left(\gamma + \alpha(1 - 2\gamma) - (1 - 2\gamma)p_t + (1 - 2\gamma)p_t^2\right). \quad (3.9)
 \end{aligned}$$

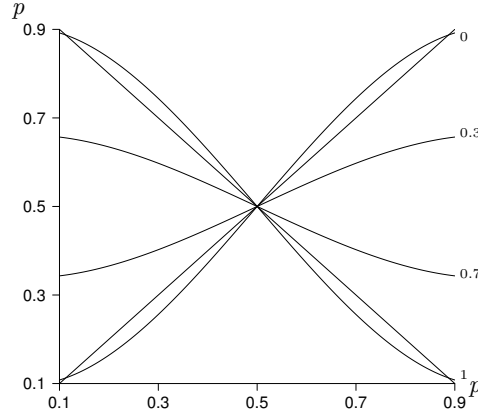


Figure 3.3: Graphs of  $f_{3;0.1,0.1;\gamma,\gamma}$  as function of  $p \in [0.1, 0.9]$ , with values  $\gamma$  as indicated at each specific graph. In addition, the diagonal and the line  $1 - p$  are drawn.

As an illustration to expression (3.9), Figure 3.3 shows a collection of graphs of  $f_{3;\alpha,\alpha;\gamma,\gamma}$  as function of  $p$ , for  $\alpha = 0.1$  and several values of  $\gamma$ .

From expression (3.9) the analysis of the generated opinion dynamics is straightforward. We give an overview.

Symmetry considerations imply that the dynamics  $\overrightarrow{f_{3;\alpha,\alpha;\gamma,\gamma}}$  has  $p = 0.5$  as an equilibrium, for any choice of  $\alpha \in [0, 0.5]$  and  $\gamma \in [0, 1]$ . In addition to parameter combinations  $\alpha$  and  $\gamma$  for which this equilibrium is unique and stable, there are combinations which allow for an unstable repelling equilibrium  $\hat{p} = 0.5$  in combination with two other, asymptotically stable, equilibria, or with two asymptotically stable periodic points of minimal period 2. Details for these possibilities to appear are derived in Appendix 3.6.4, here we confine ourselves to the outcome.

Let the *critical curves*  $c_3$  and  $C_3$  be defined as follows:

$$c_3 = \{(\alpha, \gamma) \in [0, 0.5] \times [0, 1] : (3 - 4\alpha)(1 - 2\gamma) = 2\}, \quad (3.10)$$

and

$$C_3 = \{(\alpha, \gamma) \in [0, 0.5] \times [0, 1] : (3 - 4\alpha)(1 - 2\gamma) = -2\}. \quad (3.11)$$

Figure 3.4 shows the curves  $c_3$  and  $C_3$  in the  $(\alpha, \gamma)$ -parameter space. On  $c_3$  the derivative  $f'_{3;\alpha,\alpha;\gamma,\gamma}(0.5)$  equals 1, whereas on  $C_3$  this derivative equals  $-1$ . The two

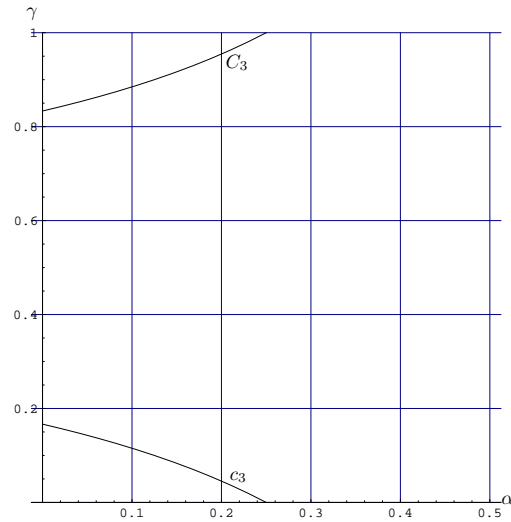


Figure 3.4: The critical curves  $c_3$  and  $C_3$  in the  $(\alpha, \gamma)$ -parameter space

corner areas in Figure 3.4 enclosed by either  $c_3$  or  $C_3$  are the regions of parameter combinations for which 0.5 is unstable; outside these regions (including the curves) 0.5 is the unique asymptotically stable equilibrium for  $\overrightarrow{f_{3;\alpha,\alpha;\gamma,\gamma}}$  independent of the initial condition. The lower left corner region is the area for which the dynamics  $\overrightarrow{f_{3;\alpha,\alpha;\gamma,\gamma}}$  has two asymptotically stable equilibria  $\hat{p}_{3;\alpha,\alpha;\gamma,\gamma}$ . Given parameter combinations  $(\alpha, \gamma)$  in this region, the opinion dynamics eventually will stabilise on an equilibrium on which the opinion with the initial majority will have maintained its majority. In case  $(\alpha, \gamma) \neq (0, 0)$ , this equilibrium is mixed; if neither inflexibles nor contrarians are present for both opinions, i.e.  $(\alpha, \gamma) = (0, 0)$ , the equilibrium is a single state attractor with only one opinion present. These results generalise those obtained in [34] for the case of equal densities of inflexibles and no contrarians for both opinions. For parameter combinations in the upper left corner region in Figure 3.4, the dynamics has two attracting periodic points of period 2. Here an initial majority does not guarantee the eventual majority, since the dynamics is such that both opinions alternately switch between minority and majority.

Thus, if both opinions are being supported by equal densities  $\alpha$  of inflexibles and equal fractions  $\gamma$  of contrarians among the floaters, for an opinion to obtain the majority it is necessary that  $\alpha$  as well as  $\gamma$  are sufficiently small, and that it has the initial majority. Also, with increasing  $\alpha$  ( $\gamma$ ), the maximum value of  $\gamma$  ( $\alpha$ ) for

which a majority is attainable decreases. If no inflexibles are present, the fraction of contrarians among the floaters must be less than approximately 17% ( $\frac{100}{6}\%$ ) for a majority to be realisable, and if the fraction of contrarians among the floaters equals 0, the density of inflexibles must be less than 25%.

If in the parameter space a combination  $(\alpha, \gamma)$  approaches from within a corner towards one of the two critical curves, then the two additional equilibria or periodic points approach towards  $p = 0.5$ ; a withdrawal in the parameter space results in the opposite movement of the additional equilibria or periodic points. It follows that when passing through  $c_3$ , the dynamics  $\overrightarrow{f_{3;\alpha,\alpha;\gamma,\gamma}}$  undergoes a supercritical pitchfork bifurcation, and when passing through  $C_3$  the dynamics undergoes a period doubling bifurcation (flip bifurcation).

### 3.4.2 The general case

We now return to the general expression (3.8) and give an overview of the possible outcomes of the dynamics  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$ . The analytical background is given in Appendix 3.6.5. We distinguish several cases.

1.  $\gamma_A + \gamma_B = 1$ .

For  $\gamma_A$  and  $\gamma_B$  such that  $\gamma_A + \gamma_B = 1$ , the function

$\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$  is quadratic in  $p$ . The corresponding opinion dynamics  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,1-\gamma_A}}$  has a unique stable equilibrium in the interval  $[\alpha_A, 1 - \alpha_B]$ .

For  $(\gamma_A, \gamma_B) = (0.5, 0.5)$ , the function  $f_{3;\alpha_A,\alpha_B;0.5,0.5}$  becomes constant and equals  $f_{3;\alpha_A,\alpha_B;0.5,0.5}(p) = 0.5(1 + \alpha_A - \alpha_B)$ ; it allows for a unique stable equilibrium  $\hat{p} = 0.5(1 + \alpha_A - \alpha_B)$ , on which opinion A has the majority if and only if  $\alpha_A > \alpha_B$ . The following figure distinguishes between parameter combinations  $\alpha_A, \alpha_B$  and  $\gamma_A$  for which the A opinion obtains either the majority or minority in equilibrium, and for which the equilibrium is approached monotonically or alternately (Figure 3.5). It follows that with increasing value of  $\gamma_A$  the region of parameter combinations  $(\alpha_A, \alpha_B)$  for which opinion A obtains the majority decreases. In addition, if  $\gamma_A \leq 0.5$ , the A opinion can obtain the majority for any value of  $\alpha_A$ , provided that  $\alpha_B$  is sufficiently small; if  $\gamma_A > 0.5$ ,  $\alpha_A$  must be sufficiently large and  $\alpha_B$  sufficiently small for an A majority to occur.



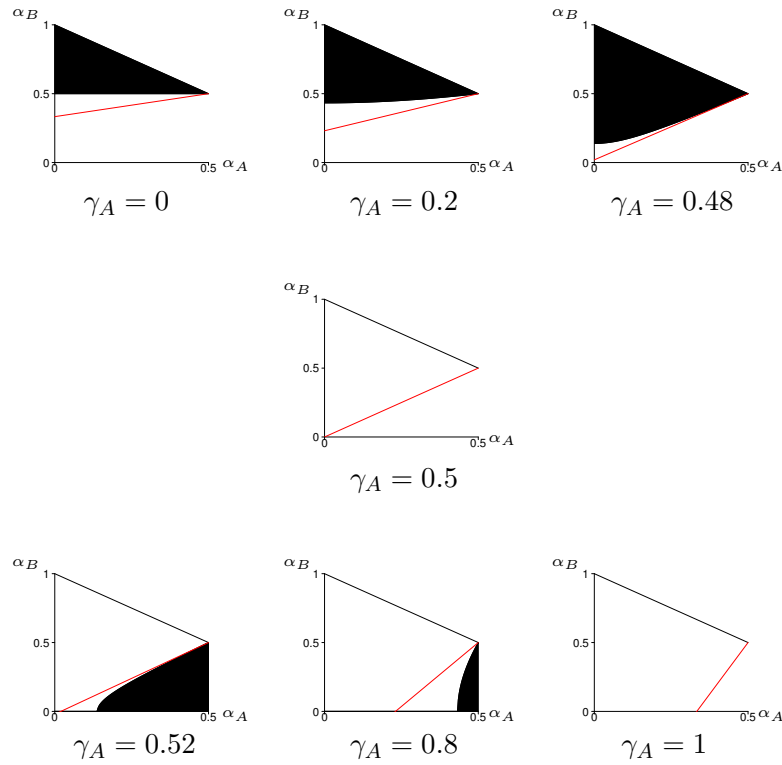


Figure 3.5: The different panes, distinguished by different values of  $\gamma_A$ , have  $\alpha_A$  on the horizontal axis and  $\alpha_B$  on the vertical one. Each pane shows the red line  $\alpha_B = \frac{1 - 2\gamma_A}{3 - 2\gamma_A} + \frac{1 + 2\gamma_A}{3 - 2\gamma_A}\alpha_A$  of parameter values  $(\alpha_A, \alpha_B)$  for which the equilibrium value  $\hat{p}_{3;\alpha_A,\alpha_B;\gamma_A,1-\gamma_A}$  equals 0.5. Below a red line the equilibrium value lies above 0.5, i.e., opinion A then obtains the majority. In addition each pane shows in white the region of parameters  $(\alpha_A, \alpha_B)$  for which the equilibrium  $\hat{p}_{3;\alpha_A,\alpha_B;\gamma_A,1-\gamma_A}$  is approached monotonically; the black regions indicate parameter combinations for which the equilibrium is approached alternately. For  $\gamma_A = 0.5$ , the derivative of  $f_{3;\alpha_A,\alpha_B;\gamma_A,1-\gamma_A}$  in the equilibrium equals 0 for all parameter values  $(\alpha_A, \alpha_B)$ , and the equilibrium is reached in one iteration. On the line  $\alpha_A + \alpha_B = 1$  the dynamics is degenerate: the density  $p$  is restricted to a single equilibrium density  $\hat{p} = \alpha_A$ . The white region  $\alpha_A + \alpha_B > 1$  is not involved in the analysis.

2.  $\gamma_A + \gamma_B \neq 1$ .

The expression  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) - p = 0$  for determining the equilibria is

$$\begin{aligned}
f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) - p = & \\
& \alpha_A(1 - \gamma_A) + (1 - \alpha_B)\gamma_B - \left(1 + 2\alpha_A(1 - 2\gamma_A) - \gamma_A + \gamma_B\right)p + \\
& \left(3 + \alpha_A(1 - 2\gamma_A) - \alpha_B(1 - 2\gamma_B) - 4\gamma_A - 2\gamma_B\right)p^2 - 2\left(1 - \gamma_A - \gamma_B\right)p^3 = 0.
\end{aligned} \tag{3.12}$$

The number of solutions is determined by its discriminant, which is denoted by  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$ . The expression for the discriminant is derived in Appendix 3.6.5; here we discuss its implications.

For parameter combinations  $(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  such that  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B) > 0$ , the equation  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) - p = 0$  has a unique real solution. If  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B) < 0$ , there are three real solutions. However, these solutions do not necessarily have to belong to the interval  $[\alpha_A, 1 - \alpha_B]$  (but if a solution lies in this interval, it clearly is an equilibrium for the dynamics  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$ ). If  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = 0$  there are three real solutions, of which at least two coincide; if this happens in the interval  $[\alpha_A, 1 - \alpha_B]$ , the parameter combination is at a bifurcation point, discriminating between dynamics with either a unique equilibrium or three equilibria. If at the bifurcation point exactly two of the three solutions coincide, the coinciding solutions form a semistable equilibrium.

Figure 3.6 shows a collection of sign plots for the discriminant, for values  $\alpha_A$  and  $\alpha_B$  as indicated, and with  $\gamma_A$  and  $\gamma_B$  for each sign plot between 0 and 1. In addition the outcome of the analysis for parameter combinations  $(\alpha_A, \alpha_B; \gamma_A, 1 - \gamma_A)$  is included, as well as the results of the analysis for combinations  $(\alpha, \alpha; \gamma, \gamma)$ .

The discriminant becomes singular for parameter combinations  $(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  with  $\gamma_A + \gamma_B = 1$ . In approaching such parameter combinations for which  $(\gamma_A, \gamma_B) \neq (0.5, 0.5)$ , the value of  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  goes to  $-\infty$ . For  $(\gamma_A, \gamma_B) = (0.5, 0.5)$ , the limit generically equals  $+\infty$  when this point is approached from the region  $\gamma_A + \gamma_B < 1$ ; the limit equals  $-\infty$  in case it is approached from the other side, i.e., from the region

$\gamma_A + \gamma_B > 1$ . (In case (0.5,0.5) is approached along the zero set of  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$ , i.e., in each pane in Figure 3.6 along the boundary that distinguishes between the yellow and green regions and touches with the line  $\gamma_A + \gamma_B = 1$ , the limit clearly equals 0.)

Our further discussion of the opinion dynamics  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$  is based on Figure 3.6. Instead of a detailed analytical treatment, we continue with a number of characteristic outcomes of the opinion dynamics.

A first characteristic that draws attention in Figure 3.6 is the existence of a wedge-shaped region of parameter combinations  $(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  with negative discriminant for sufficiently small values of all four parameters. For the cases with both  $\alpha_A = \alpha_B$  and  $\gamma_A = \gamma_B$  within this region, we already found the existence of two attracting equilibria, symmetrically positioned with respect to a third, unstable equilibrium 0.5. We therefore expect also to find a similar pattern of three equilibria in  $[\alpha_A, 1 - \alpha_B]$  for deviations from such symmetric cases within the wedge-shaped region. In [34] it has been derived that this is indeed the case in the absence of contrarians, i.e., for parameter combinations for which  $\gamma_A = \gamma_B = 0$ , and for  $\alpha_A$  and  $\alpha_B$  sufficiently small. Figure 3.7, which shows a number of graphs of functions  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  for relatively small values  $\alpha_A, \alpha_B, \gamma_A$  and  $\gamma_B$ , implies the same pattern: in case the determinant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  is negative, the opinion dynamics has two attracting equilibria that are separated by an unstable one. The two attracting equilibria differ with respect to the opinion by which they are dominated. By leaving the wedge-shaped area, a bifurcation in the opinion dynamics occurs on its boundary  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = 0$ . Generically, when moving from inside the wedge-shaped area towards this boundary, the unstable equilibrium and one of the two stable equilibria move towards each other, and at the bifurcation point merge (thus causing a supercritical saddle-node bifurcation). Once the boundary has been crossed, the region of parameters with a positive discriminant is entered, and the dynamics is left with one attracting equilibrium. On this equilibrium opinion  $A$  dominates if the upper part of the boundary is crossed, i.e., when  $\gamma_B > \gamma_A$ ; opinion  $B$  has the majority when the right-hand side of the boundary is passed, on which  $\gamma_A > \gamma_B$  holds. This is also illustrated in Figure 3.7. The occurrence of such a bifurcation may lead to a drastic change in the outcome of the opinion dynamics: whereas inside the wedge-shaped region

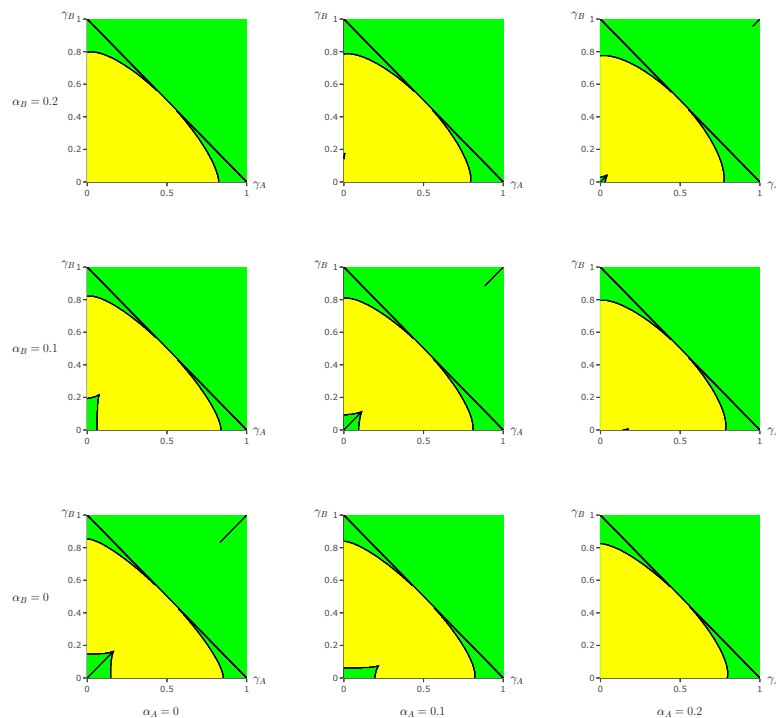


Figure 3.6: A collection of panes, for values  $\alpha_A$  and  $\alpha_B$  as indicated, and  $\gamma_A$  and  $\gamma_B$  for each pane ranging between 0 and 1, with  $\gamma_A$  on the horizontal axis and  $\gamma_B$  on the vertical axis. In each pane the sign plot of the discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  is shown for points  $(\gamma_A, \gamma_B)$  for which  $\gamma_A + \gamma_B \neq 1$ . Yellow areas represent the parameter combinations with a positive discriminant (i.e., combinations for which the corresponding opinion dynamics has a unique equilibrium), and in green regions the discriminant is negative (the corresponding opinion dynamics then has 3 different equilibria, but not necessarily in the interval  $[\alpha_A, 1 - \alpha_B]$ ). On the curve separating the yellow and green region the discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  for the third-degree function  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}(p) - p$  equals 0 (except in  $(\gamma_A, \gamma_B) = (0.5, 0.5)$ , where this function becomes quadratic). In each pane the line  $\gamma_A + \gamma_B = 1$  is drawn in black. On these lines the third-degree function  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}$  becomes quadratic and the corresponding dynamics has a unique equilibrium increasing from 0 (for  $\gamma_A = 1$ ) to 1 ( $\gamma_A = 0$ ). Furthermore, in panes for which  $\alpha_A = \alpha_B$  holds, on the line  $\gamma_A = \gamma_B$  in the green regions (i.e., a negative discriminant) in black the points are indicated for which the equilibrium  $\hat{p} = 0.5$  for  $\overrightarrow{f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}}$  is unstable; other points on the lines  $\gamma_A = \gamma_B$  (for  $\alpha_A = \alpha_B$ ) indicate parameter combinations for which  $\hat{p} = 0.5$  is stable (as follows from Figure 3.4).

the outcome of the opinion dynamics depends on the initial condition, outside the wedge-shaped area the opinion dynamics will end on the unique equilibrium,

independent of the initial condition. At the bifurcation point at the endpoint of the sharp region of the wedge-shaped area a supercritical pitchfork bifurcation occurs, in which the three equilibria merge together into one attracting equilibrium.

The yellow regions in Figure 3.6 are formed by the parameter combinations for which the discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  is positive. The corresponding opinion dynamics then have a unique equilibrium, which (for the parameter combinations in Figure 3.6) is approached monotonically. Figure 3.8 shows a number of graphs  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}$  for parameter combinations with a positive discriminant. The Figure indicates that for small values of  $\gamma_A$  and large values of  $\gamma_B$  opinion  $A$  dominates in equilibrium, and that the dominion shift towards the alternative opinion if the fraction of contrarians among the  $A$  floaters increases and that among the  $B$  floaters decreases.

For given parameters  $\alpha_A$  and  $\alpha_B$ , crossing the boundary of the yellow area in any direction away from the lower left corner leads to the occurrence of a saddle-node bifurcation, now however outside the domain  $[\alpha_A, 1 - \alpha_B]$  of the functions  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}$  (maintaining an attracting equilibrium in the domain). Therefore in the green region thus entered, the opinion dynamics also is characterised by a unique attracting equilibrium. Proceeding towards the upper right corner, the line of parameter combinations  $(\gamma_A, \gamma_B)$  satisfying  $\gamma_A + \gamma_B = 1$  is crossed. On this line the discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  is singular, and the corresponding opinion dynamics have been analysed in 3.4.2.1.

In the green area in the upper right corner, for equal and sufficiently small values  $\alpha_A = \alpha_B = \alpha$  and sufficiently large and equal values  $\gamma_A = \gamma_B = \gamma$  it has been derived earlier that  $\overrightarrow{f_{\alpha_A, \alpha_B; \gamma_A, \gamma_B}}$  has a unique unstable equilibrium  $\hat{p} = 0.5$ , which causes the convergence of the dynamics towards an attracting periodic orbit of period 2. Neither of the two opinions then achieves the definite majority. The values  $\alpha$  and  $\gamma$  for which this occurs have been derived in 3.4.1, and are represented in Figure 3.6 by black line segments in the upper right corners. For these parameter combinations the discriminant of the equation  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}(p) - p = 0$  is negative and thus has three different solutions, of which two are situated outside the domain  $[\alpha_A, 1 - \alpha_B]$ . Continuity arguments imply that this behaviour will be maintained for parameter combinations sufficiently close to these line segments. Figure 3.9 illustrates this. If the parameter combinations are sufficiently far removed from

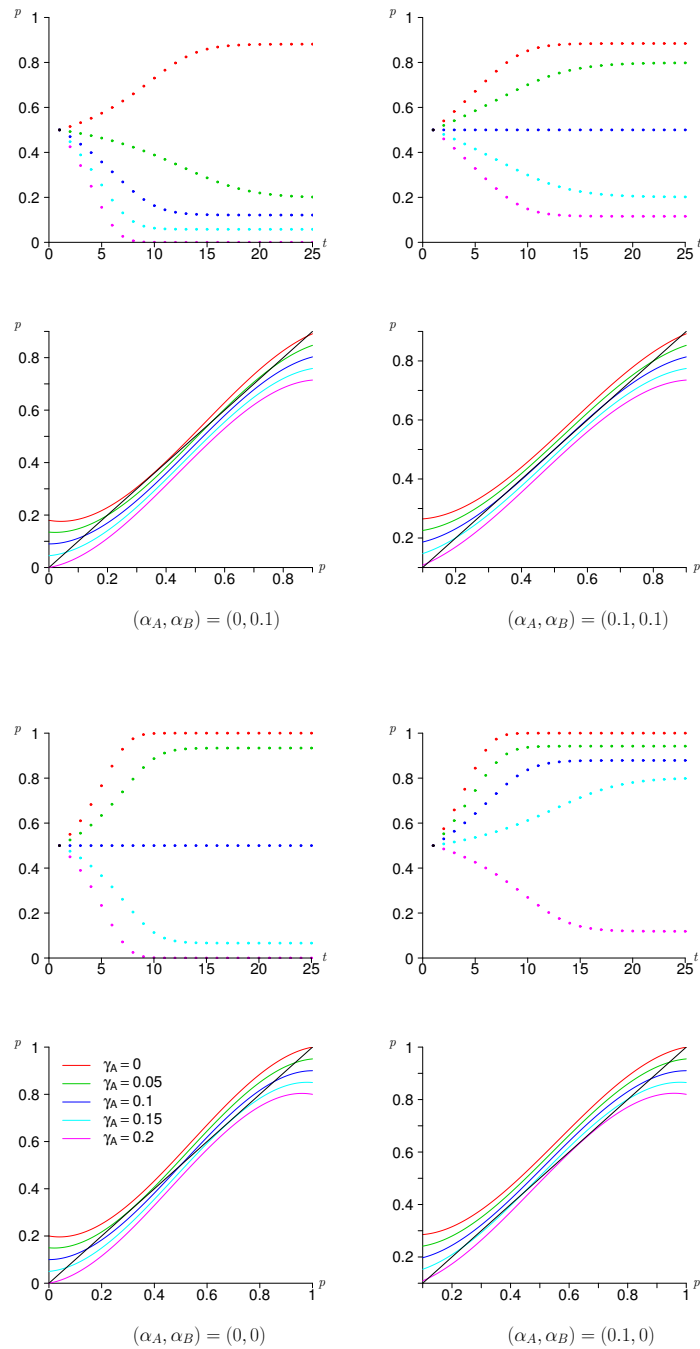


Figure 3.7: Four panes of graphs of functions  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  for relatively small values  $\alpha_A, \alpha_B, \gamma_A$  and  $\gamma_B$ , with  $(\alpha_A, \alpha_B)$  as indicated below each pane, and with values  $\gamma_A$  as indicated by the color code. In each of the four panes,  $\gamma_A$  and  $\gamma_B$  satisfy  $\gamma_A + \gamma_B = 0.2$ . I.e., in the corresponding panes in Figure 3.6 we traverse the line  $\gamma_A + \gamma_B = 0.2$  from its upper left point on the  $\gamma_A = 0$  axis to its lower right point on the  $\gamma_B = 0$  axis, thus passing through regions with positive, zero as well as negative discriminant. Above each of these panes the values of the densities for opinion A in subsequent time steps are plotted, as obtained by the corresponding opinion dynamics  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$ , with initial density  $p = 0.5$ .

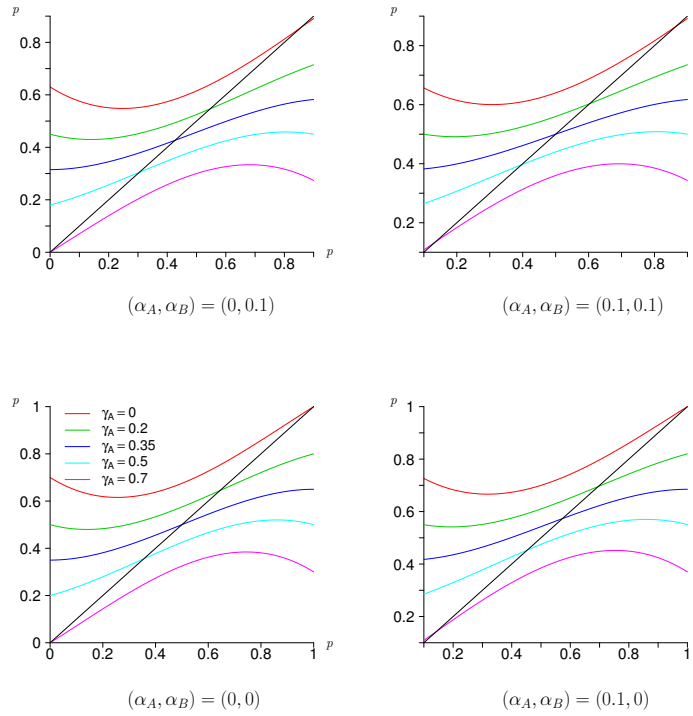


Figure 3.8: Four panes of graphs of functions  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}$  for relatively small values  $\alpha_A$  and  $\alpha_B$  as indicated, and  $\gamma_A$ -values as given by the color code.  $\gamma_A$  and  $\gamma_B$  satisfy  $\gamma_A + \gamma_B = 0.7$ , i.e. for given  $(\alpha_A, \alpha_B)$ , we traverse the line  $\gamma_A + \gamma_B = 0.7$  from its upper left point on the  $\gamma_A = 0$  line to its lower right point on the  $\gamma_B = 0$  line. The discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  for the exposed parameter values is positive, indicating a unique equilibrium for the corresponding opinion dynamics.

these line segments but  $\gamma_A$  and  $\gamma_B$  are still relatively large (i.e., for given  $\alpha_A$  and  $\alpha_B$ , in the upper right corner), the dynamics will converge alternately to a unique equilibrium. I.e., by moving away from the manifold determined by the constraints  $\alpha_A = \alpha_B$  and  $\gamma_A = \gamma_B$  with large values  $\gamma_A$  and  $\gamma_B$ , a flip bifurcation occurs in which the attracting periodic 2 orbit collapses to an attracting equilibrium point. This is illustrated by Figure 3.10. On the attractor the dominion shifts towards opinion  $B$  with increasing  $\gamma_A$  and decreasing  $\gamma_B$ .

We end our discussion by presenting some additional opinion dynamics  $\overrightarrow{f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}}$  for parameter combinations from both the regions with positive and negative discriminant. We remark here that the line segments on the line  $\gamma_A = \gamma_B$  in the lower left and upper right regions of the sign plots of  $D(\alpha, \alpha; \gamma_A, \gamma_B)$  disappear for  $\alpha \geq 0.25$ . For choices  $(\alpha_A, \alpha_B)$  outside the region for which both

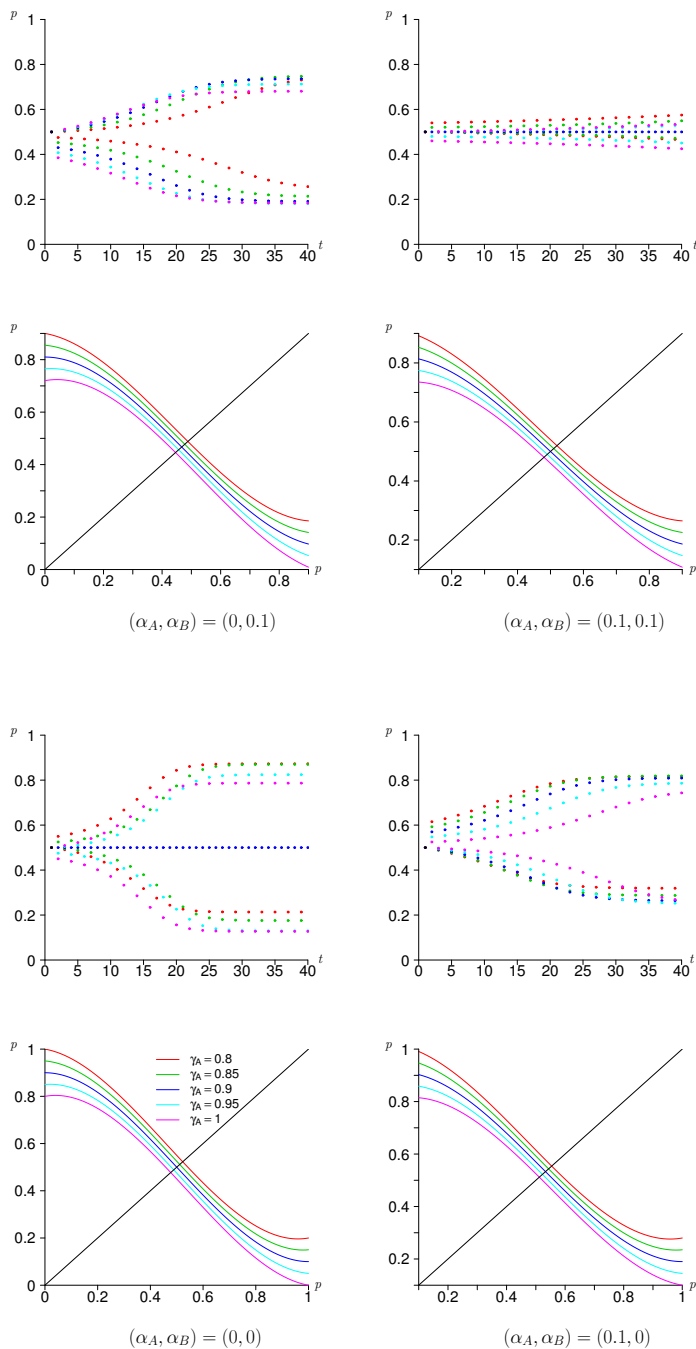


Figure 3.9: Four panes of graphs of functions  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  for relatively small values  $\alpha_A$  and  $\alpha_B$ , and with  $\gamma_A$  and  $\gamma_B$  satisfying  $\gamma_A + \gamma_B = 1.8$ . The values of  $\alpha_A$  and  $\alpha_B$  are indicated below each of the four panes, and values for  $\gamma_A$  are as indicated by the color code. I.e., for given  $(\alpha_A, \alpha_B)$ , we traverse the line  $\gamma_A + \gamma_B = 1.8$  from its upper left point on the  $\gamma_B = 1$  line to its lower right point on the  $\gamma_A = 1$  line. Above each of these panes the densities for opinion A are again presented, as obtained by the corresponding opinion dynamics  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  with initial density  $p = 0.5$ .



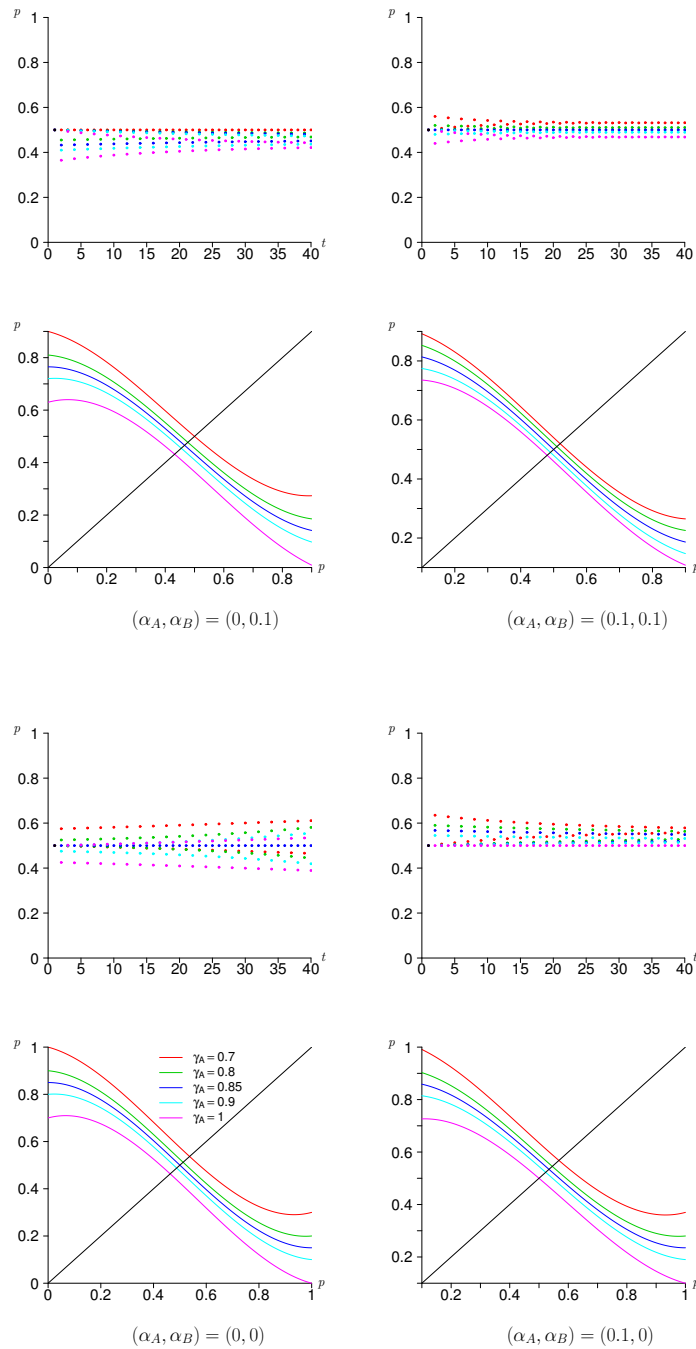


Figure 3.10: Four panes of graphs of functions  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  for relatively small values  $\alpha_A$  and  $\alpha_B$ , and with  $\gamma_A$  and  $\gamma_B$  satisfying  $\gamma_A + \gamma_B = 1.7$ . The values of  $\alpha_A$  and  $\alpha_B$  are indicated below each of the four panes, values for  $\gamma_A$  are again given by the color code. For given  $(\alpha_A, \alpha_B)$  values of  $\gamma_A$  are such that we traverse the line  $\gamma_A + \gamma_B = 1.7$  from its upper left point on the  $\gamma_B = 1$  line to its lower right point on the  $\gamma_A = 1$  line. Above each pane the densities for opinion A are presented, as obtained by the corresponding opinion dynamics  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$ , with initial density  $p = 0.5$ .

$\alpha_A \leq 0.25$  and  $\alpha_B \leq 0.25$  there is no qualitative change in the sign plots of  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$ , and we choose to restrict and illustrate this for the choices  $(\alpha_A, \alpha_B) = (0.1, 0.4)$  and  $(\alpha_A, \alpha_B) = (0.5, 0.3)$ , i.e., a case with small  $\alpha_A$  and intermediate  $\alpha_B$ , and one with both  $\alpha_A$  and  $\alpha_B$  intermediate. Figure 3.11 shows the sign plots of the discriminants  $D(0.1, 0.4; \gamma_A, \gamma_B)$  (a) and  $D(0.5, 0.3; \gamma_A, \gamma_B)$  (b).

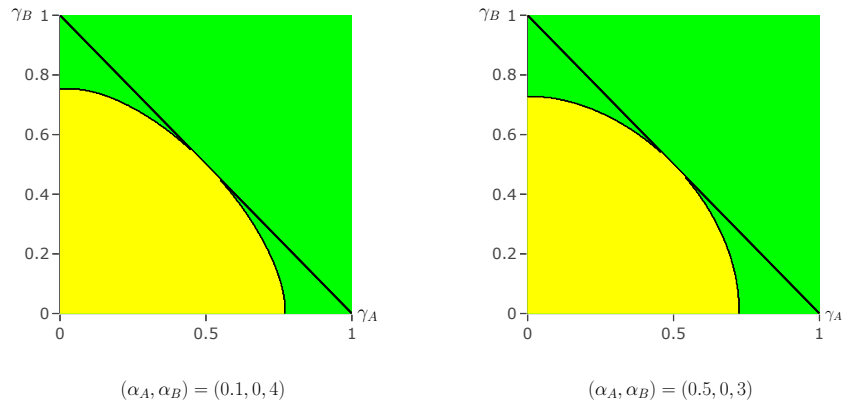


Figure 3.11: Sign plots of the discriminants  $D(0.1, 0.4; \gamma_A, \gamma_B)$  (a) and  $D(0.5, 0.3; \gamma_A, \gamma_B)$  (b). The color code is as in Fig. 3.6. On the curve separating the yellow and green region the discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  for the third-degree function  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}(p) - p$  again equals 0 (except in  $(\gamma_A, \gamma_B) = (0.5, 0.5)$ , where this function becomes quadratic). In addition in each pane the line  $\gamma_A + \gamma_B = 1$  is drawn in black.

The corresponding graphs of  $f_{3; \alpha_A, \alpha_B; \gamma_A, \gamma_B}$  are represented in Figures 3.12 and 3.13, for several values of  $\gamma_A$  and  $\gamma_B$ . All cases allow for a unique attracting equilibrium. High values of both  $\gamma_A$  and  $\gamma_B$  lead to alternating convergence. Furthermore, a decrease in the fraction of contrarians among the floaters of an opinion increases the density of this opinion in equilibrium.

### 3.5 CONCLUSIONS

The results presented re-establish those derived in [23, 28], which concerned communities of non-contrarian and contrarian floaters, and [34], which studied the combined effects of inflexibles and non-contrarian floaters. The distinctive

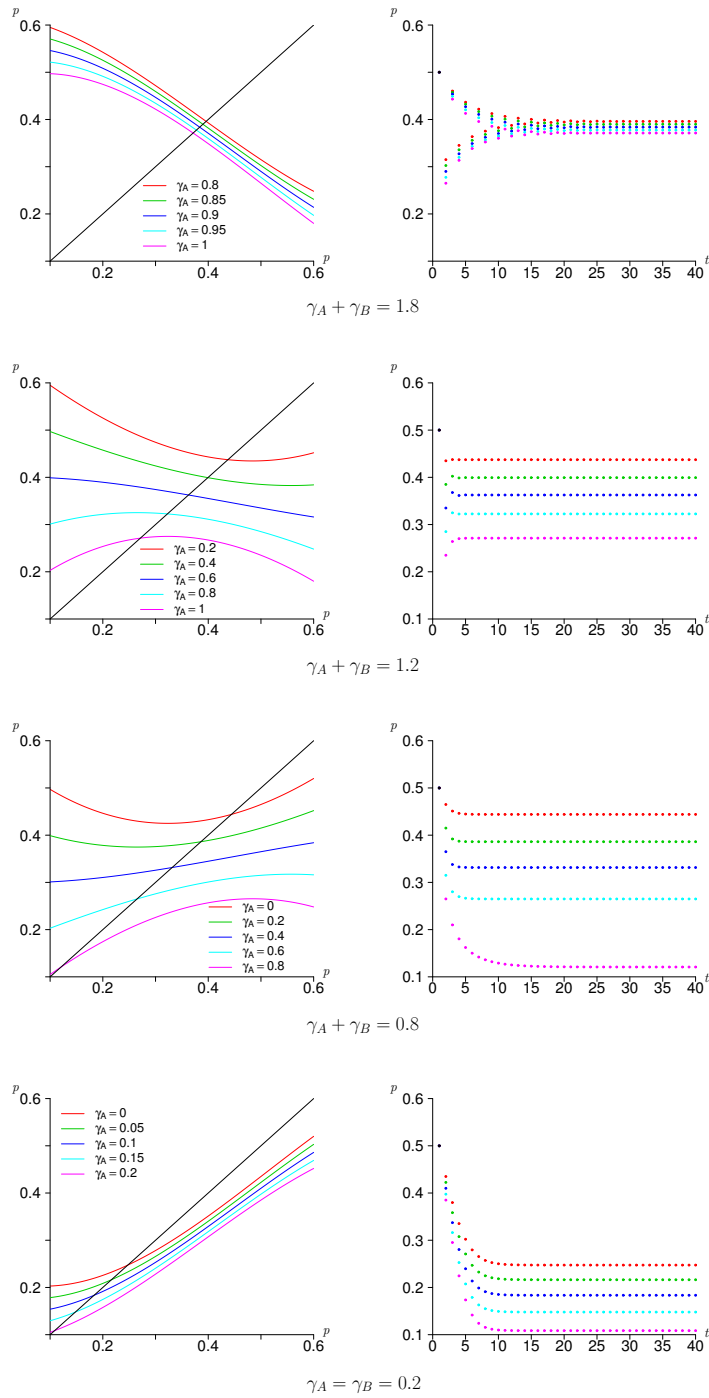


Figure 3.12: The left column shows four panes of graphs of functions  $f_{3;0.1,0.4;\gamma_A,\gamma_B}$ , for different combinations of  $\gamma_A$  and  $\gamma_B$ , with  $\gamma_A$  as indicated and per row of graphs  $\gamma_B$  such that the relation mentioned below the row of graphs is satisfied. The right column of the Figure shows the densities of opinion  $A$  as generated by the corresponding opinion dynamics for initial value  $p = 0.5$ .

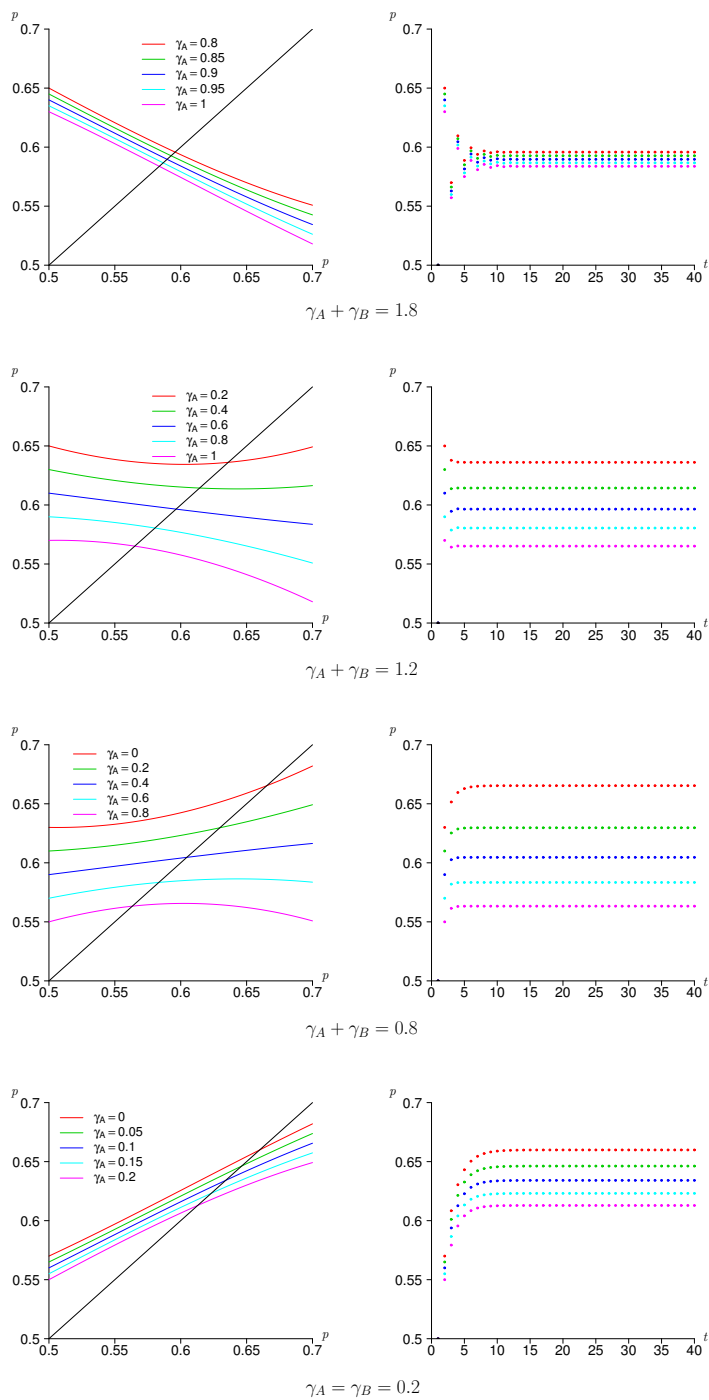


Figure 3.13: The left column shows four panes of graphs of functions  $f_{3;0.5,0.3;\gamma_A,\gamma_B}$  for the same combinations of  $\gamma_A$  and  $\gamma_B$  as in Fig. 3.12. The right column of the Figure shows the densities of opinion A as generated by the corresponding opinion dynamics for initial value  $p = 0.5$ .

patterns of opinion dynamics are not characterised by complete quantitative detail. Rather, the results intend to point to possible outcomes of opinion dynamics. We conclude that various kinds of dynamics may occur. In case the local majority rule followed by the contrarian changes are applied for group sizes  $L = 1$  or  $2$ , the opinion dynamics generically converges to a unique equilibrium. In case the sum of fractions of contrarians for the two opinions is larger than  $1$ , the equilibrium generically is approached alternately, otherwise the dynamics generically shows a monotone approach. For an opinion to obtain the majority in equilibrium, it is required that this opinion is supported by a sufficiently large density of inflexibles in combination with a sufficiently small fraction of contrarians, as expressed by condition (3.5).

Group size  $L = 3$  allows for additional outcomes for the opinion dynamics. For sufficiently small densities of inflexibles for both opinions, and in addition sufficiently small fractions of contrarians among the floaters for the two opinions, the dynamics allows for two attracting equilibria, that differ in which opinion has the majority. The opinion that eventually will achieve the majority thus is determined by the initial condition, and an opinion that has a fraction of contrarians that is sufficiently smaller than that of the alternative opinion, may achieve the majority in equilibrium, although initially it may be present as a minority. For small values of inflexibles in combination with sufficiently large fractions of contrarians among the floaters, the generated opinion dynamics causes alternating convergence to a period 2 stable orbit (Figure 3.9). An increase of the densities of inflexibles or a slight lowering of at least one of the fractions of contrarians causes the collapse of the attracting periodic orbit into an equilibrium, but maintains the alternating behaviour (Figure 3.10). For a relatively large collection of parameter combinations the dynamics ends up on a unique attracting equilibrium, which is approached either monotonically or alternating (see e.g. Figures 3.5 and 3.13). An increase in the fraction of contrarians among the floaters of an opinion leads to a decrease of the density of that opinion in equilibrium. Thus, for an opinion to achieve the majority in equilibrium, a small fraction of contrarians among its floaters is favourable.

In [28], the “hung elections” outcome in several national votes has been discussed in terms of the interplay of non-contrarian and contrarian floaters. Likewise, the

present paper may shed a light on the (dis)appearance of alternating opinion dynamics. An alternating series of wins and losses of the majority for two political opinions in pre-election polls may point to considerable fractions of contrarians among the floaters on both sides. In case the alternating pattern converges to a stable period 2 cycle, the uncertainty who will win the election will linger on until the final decisive event. (Note that since the outcome of an election in an alternating environment depends on the moment the election actually takes place, it may happen that in subsequent polls the same winner occurs. This is however no indication of sustained major support. Furthermore, in a sequence of alternating environments, a large number of subsequent wins for the same opinion seems unlikely.) If however the alternating changes are converging to an equilibrium, one of the opinions eventually will reach a decisive majority. Due to the sensitivity of politics for influences, a change in parameter values may easily occur, either with respect to the densities of inflexibles or to the fractions of contrarians. This may result in a switch from the one alternating pattern into the other one, or even into monotone convergence towards an equilibrium. Although our framework does not map unequivocally to real communities, we think it may hint at possible explanations of outcomes of opinion dynamics.

In forthcoming papers we plan to continue the study of opinion dynamics, by focusing on communities in which more than two opinions are being supported, and by taking into account geographic networks.

## 3.6 APPENDICES

Subsections 3.6.1, 3.6.2 and 3.6.3 present tables for groups of sizes  $L = 1, 2$  and  $3$  from which the density of the  $A$  opinion is derived after application of the l.m.r. and the switch by the contrarians, given an initial density  $p$  for the  $A$  opinion. Each table consists of four columns, of which the first four are separated by arrows. The first column gives the possible group compositions in terms of inflexibles and non-contrarian and/or contrarian floaters, the second column gives the effect of the application of the l.m.r. for the group compositions given in the first column. An application is indicated by a horizontal arrow, whose first appearance in a table is indexed by "l.m.r."; at other places in the tables this index is omitted. The third column then gives the effect of the switches by the contrarians if applicable, where it is understood that a contrarian switches into a floater of the alternative opinion. The final column gives the contributions of the effect of the l.m.r. and the presence of the contrarians to the density of the  $A$  opinion, weighed with the probability of the original group composition in the ensemble of all possible groups of fixed size, given the densities  $\alpha_A$  and  $\alpha_B$  of the inflexibles for both opinions, the fractions  $\gamma_A$  and  $\gamma_B$  of contrarians among the floaters of the  $A$  and  $B$  opinion, respectively, and the densities  $p - \alpha_A$  for the  $A$  floaters and  $1 - \alpha_B - p$  for the  $B$  floaters. The total sum of these contributions yields  $f_{L;\alpha_A,\alpha_B,\gamma_A,\gamma_B}(p)$ . After each opinion update, all supporters for both opinions are recollected and then redistributed again, either as inflexible or as a non-contrarian or contrarian floater, according to the fixed densities for inflexibles and the fixed fractions of contrarians for the two opinions. In each table the following notation is being used:

- $A_i$  inflexible of the  $A$  opinion,
- $A_f$  floater of the  $A$  opinion,
- $A_{nc}$  non-contrarian floater of the  $A$  opinion,
- $A_c$  contrarian floater of the  $A$  opinion,
- $A_{f_{nc}}$  floater of the  $A$  opinion coming from a  $B$  non-contrarian floater after application of the l.m.r.,
- $A_{f_c}$  floater of the  $A$  opinion coming from a  $B$  contrarian floater after application of the l.m.r.,

and

- $B_i$  inflexible of the  $B$  opinion,  
 $B_f$  floater of the  $B$  opinion,  
 $B_{nc}$  non-contrarian floater of the  $B$  opinion,  
 $B_c$  contrarian floater of the  $B$  opinion,  
 $B_{f_{nc}}$  floater of the  $B$  opinion coming from a  $A$  non-contrarian floater after application of the l.m.r.,  
 $B_{f_c}$  floater of the  $B$  opinion coming from a  $A$  contrarian floater after application of the l.m.r..

3.6.1 Table 1: group size  $L = 1$

Table 1	
$A_i \xrightarrow{l.m.r.} A_i$	$\alpha_A$
$A_{nc} \rightarrow A_{nc}$	$(1 - \gamma_A)(p - \alpha_A)$
$A_c \rightarrow A_c \rightarrow B_f$	0
$B_i \rightarrow B_i$	0
$B_{nc} \rightarrow B_{nc}$	0
$B_c \rightarrow B_c \rightarrow A_f$	$\gamma_B(1 - \alpha_B - p)$



3.6.2 Table 2: group size  $L = 2$ 

$A_i, A_i \xrightarrow{l.m.r.} A_i, A_i$	$\alpha_A^2$
$A_i, A_{nc} \rightarrow A_i, A_{nc}$	$2\alpha_A(1 - \gamma_A)(p - \alpha_A)$
$A_i, A_c \rightarrow A_i, A_c \rightarrow A_i, B_f$	$\alpha_A\gamma_A(p - \alpha_A)$
$A_i, B_i \rightarrow A_i, B_i$	$\alpha_A\alpha_B$
$A_i, B_{nc} \rightarrow A_i, B_{nc}$	$\alpha_A(1 - \gamma_B)(1 - \alpha_B - p)$
$A_i, B_c \rightarrow A_i, B_c \rightarrow A_i, A_f$	$2\alpha_A\gamma_B(1 - \alpha_B - p)$
$A_{nc}, A_{nc} \rightarrow A_{nc}, A_{nc}$	$(1 - \gamma_A)^2(p - \alpha_A)^2$
$A_{nc}, A_c \rightarrow A_{nc}, A_c \rightarrow A_{nc}, B_f$	$\gamma_A(1 - \gamma_A)(p - \alpha_A)^2$
$A_{nc}, B_i \rightarrow A_{nc}, B_i$	$\alpha_B(1 - \gamma_A)(p - \alpha_A)$
$A_{nc}, B_{nc} \rightarrow A_{nc}, B_{nc}$	$(1 - \gamma_A)(1 - \gamma_B)(p - \alpha_A)(1 - \alpha_B - p)$
$A_{nc}, B_c \rightarrow A_{nc}, B_c \rightarrow A_{nc}, A_f$	$2(1 - \gamma_A)\gamma_B(p - \alpha_A)(1 - \alpha_B - p)$
$A_c, A_c \rightarrow A_c, A_c \rightarrow B_f, B_f$	0
$A_c, B_i \rightarrow A_c, B_i \rightarrow B_f, B_i$	0
$A_c, B_{nc} \rightarrow A_c, B_{nc} \rightarrow B_f, B_{nc}$	0
$A_c, B_c \rightarrow A_c, B_c \rightarrow B_f, A_f$	$\gamma_A\gamma_B(p - \alpha_A)(1 - \alpha_B - p)$
$B_i, B_i \rightarrow B_i, B_i$	0
$B_i, B_{nc} \rightarrow B_i, B_{nc}$	0
$B_i, B_c \rightarrow B_i, B_c \rightarrow B_i, A_f$	$\alpha_B\gamma_B(1 - \alpha_B - p)$
$B_{nc}, B_{nc} \rightarrow B_{nc}, B_{nc}$	0
$B_{nc}, B_c \rightarrow B_{nc}, B_c \rightarrow B_{nc}, A_f$	$\gamma_B(1 - \gamma_B)(1 - \alpha_B - p)^2$
$B_c, B_c \rightarrow B_c, B_c \rightarrow A_f, A_f$	$\gamma_B^2(1 - \alpha_B - p)^2$

3.6.3 Table 3: group size  $L = 3$ 

Table 3

$A_i, A_i, A_i \xrightarrow{l.m.r.} A_i, A_i, A_i$	$\alpha_A^3$
$A_i, A_i, A_{nc} \rightarrow A_i, A_i, A_{nc}$	$3\alpha_A^2(1 - \gamma_A)(p - \alpha_A)$
$A_i, A_i, A_c \rightarrow A_i, A_i, A_c \rightarrow A_i, A_i, B_f$	$2\alpha_A^2\gamma_A(p - \alpha_A)$
$A_i, A_i, B_i \rightarrow A_i, A_i, B_i$	$2\alpha_A^2\alpha_B$
$A_i, A_i, B_{nc} \rightarrow A_i, A_i, A_f$	$3\alpha_A^2(1 - \gamma_B)(1 - \alpha_B - p)$
$A_i, A_i, B_c \rightarrow A_i, A_i, A_{fc} \rightarrow A_i, A_i, B_f$	$2\alpha_A^2\gamma_B(1 - \alpha_B - p)$
$A_i, A_{nc}, A_{nc} \rightarrow A_i, A_{nc}, A_{nc}$	$3\alpha_A(1 - \gamma_A)^2(p - \alpha_A)^2$
$A_i, A_{nc}, A_c \rightarrow A_i, A_{nc}, A_c \rightarrow A_i, A_{nc}, B_f$	$4\alpha_A\gamma_A(1 - \gamma_A)(p - \alpha_A)^2$
$A_i, A_{nc}, B_i \rightarrow A_i, A_{nc}, B_i$	$4\alpha_A\alpha_B(1 - \gamma_A)(p - \alpha_A)$
$A_i, A_{nc}, B_{nc} \rightarrow A_i, A_{nc}, A_f$	$6\alpha_A(1 - \gamma_A)(1 - \gamma_B)(p - \alpha_A) \times$ $(1 - \alpha_B - p)$
$A_i, A_{nc}, B_c \rightarrow A_i, A_{nc}, A_{fc} \rightarrow A_i, A_{nc}, B_f$	$4\alpha_A\gamma_B(1 - \gamma_A)(p - \alpha_A) \times$ $(1 - \alpha_B - p)$
$A_i, A_c, A_c \rightarrow A_i, A_c, A_c \rightarrow A_i, B_f, B_f$	$\alpha_A\gamma_A^2(p - \alpha_A)^2$
$A_i, A_c, B_i \rightarrow A_i, A_c, B_i \rightarrow A_i, B_f, B_i$	$2\alpha_A\alpha_B\gamma_A(p - \alpha_A)$
$A_i, A_c, B_{nc} \rightarrow A_i, A_c, A_f \rightarrow A_i, B_f, A_f$	$4\alpha_A\gamma_A(1 - \gamma_B)(p - \alpha_A) \times$ $(1 - \alpha_B - p)$
$A_i, A_c, B_c \rightarrow A_i, A_c, A_{fc} \rightarrow A_i, B_f, B_f$	$2\alpha_A\gamma_A\gamma_B(p - \alpha_A) \times$ $(1 - \alpha_B - p)$
$A_i, B_i, B_i \rightarrow A_i, B_i, B_i$	$\alpha_A\alpha_B^2$
$A_i, B_i, B_{nc} \rightarrow A_i, B_i, B_{nc}$	$2\alpha_A\alpha_B(1 - \gamma_B)(1 - \alpha_B - p)$
$A_i, B_i, B_c \rightarrow A_i, B_i, B_c \rightarrow A_i, B_i, A_f$	$4\alpha_A\alpha_B\gamma_B(1 - \alpha_B - p)^2$
$A_i, B_{nc}, B_{nc} \rightarrow A_i, B_{nc}, B_{nc}$	$\alpha_A(1 - \gamma_B)^2(1 - \alpha_B - p)^2$
$A_i, B_{nc}, B_c \rightarrow A_i, B_{nc}, B_c \rightarrow A_i, B_{nc}, A_f$	$4\alpha_A\gamma_B(1 - \gamma_B)(1 - \alpha_B - p)^2$
$A_i, B_c, B_c \rightarrow A_i, B_c, B_c \rightarrow A_i, A_f, A_f$	$3\alpha_A\gamma_B^2(1 - \alpha_B - p)^2$
$A_{nc}, A_{nc}, A_{nc} \rightarrow A_{nc}, A_{nc}, A_{nc}$	$(1 - \gamma_A)^3(p - \alpha_A)^3$
$A_{nc}, A_{nc}, A_c \rightarrow A_{nc}, A_{nc}, A_c \rightarrow A_{nc}, A_{nc}, B_f$	$2\gamma_A(1 - \gamma_A)^2(p - \alpha_A)^3$
$A_{nc}, A_{nc}, B_i \rightarrow A_{nc}, A_{nc}, A_f$	$2\alpha_B(1 - \gamma_A)^2(p - \alpha_A)^2$
$A_{nc}, A_{nc}, B_{nc} \rightarrow A_{nc}, A_{nc}, A_f$	$3(1 - \gamma_A)^2(1 - \gamma_B)(p - \alpha_A)^2 \times$ $(1 - \alpha_B - p)$
$A_{nc}, A_{nc}, B_c \rightarrow A_{nc}, A_{nc}, A_{fc} \rightarrow A_{nc}, A_{nc}, B_f$	$2\gamma_B(1 - \gamma_A)^2(p - \alpha_A)^2 \times$ $(1 - \alpha_B - p)$
$A_{nc}, A_c, A_c \rightarrow A_{nc}, A_c, A_c \rightarrow A_{nc}, B_f, B_f$	$(1 - \gamma_A)\gamma_A^2(p - \alpha_A)^2$
$A_{nc}, A_c, B_i \rightarrow A_{nc}, A_c, B_i \rightarrow A_{nc}, B_f, B_i$	$2\alpha_B\gamma_A(1 - \gamma_A)(p - \alpha_A)^2$
$A_{nc}, A_c, B_{nc} \rightarrow A_{nc}, A_c, A_f \rightarrow A_{nc}, B_f, A_f$	$4\gamma_A(1 - \gamma_A)(1 - \gamma_B)(p - \alpha_A)^2 \times$ $(1 - \alpha_B - p)$
$A_{nc}, A_c, B_c \rightarrow A_{nc}, A_c, A_{fc} \rightarrow A_{nc}, B_f, B_f$	$2\gamma_A\gamma_B(1 - \gamma_A)(p - \alpha_A)^2 \times$ $(1 - \alpha_B - p)$

Table 3 (continued)

$A_{nc}, B_i, B_i \rightarrow B_f, B_i, B_i$	0
$A_{nc}, B_i, B_{nc} \rightarrow B_f, B_i, B_{nc}$	0
$A_{nc}, B_i, B_c \rightarrow B_f, B_i, B_c \rightarrow B_f, B_i, A_f$	$2\alpha_B\gamma_B(1 - \gamma_A)(p - \alpha_A) \times$ $(1 - \alpha_B - p)$
$A_{nc}, B_{nc}, B_{nc} \rightarrow B_f, B_{nc}, B_{nc}$	0
$A_{nc}, B_{nc}, B_c \rightarrow B_f, B_{nc}, B_c \rightarrow B_f, B_{nc}, A_f$	$2\gamma_B(1 - \gamma_A)(1 - \gamma_B)(p - \alpha_A) \times$ $(1 - \alpha_B - p)^2$
$A_{nc}, B_c, B_c \rightarrow B_f, B_c, B_c \rightarrow B_f, A_f, A_f$	$2(1 - \gamma_A)\gamma_B^2(p - \alpha_A)(1 - \alpha_B - p)^2$
$A_c, A_c, A_c \rightarrow A_c, A_c, A_c \rightarrow B_f, B_f, B_f$	0
$A_c, A_c, B_i \rightarrow A_c, A_c, B_i \rightarrow B_f, B_f, B_i$	0
$A_c, A_c, B_{nc} \rightarrow A_c, A_c, A_f \rightarrow B_f, B_f, A_f$	$(1 - \gamma_A)\gamma_A^2(p - \alpha_A)^2(1 - \alpha_B - p)$
$A_c, A_c, B_c \rightarrow A_c, A_c, A_{fc} \rightarrow B_f, B_f, B_f$	0
$A_c, B_i, B_i \rightarrow B_{fc}, B_i, B_i \rightarrow A_f, B_i, B_i$	$\alpha_B^2\gamma_A(p - \alpha_A)$
$A_c, B_i, B_{nc} \rightarrow B_{fc}, B_i, B_{nc} \rightarrow A_f, B_i, B_{nc}$	$2\alpha_B\gamma_A(1 - \gamma_B)(p - \alpha_A)(1 - \alpha_B - p)$
$A_c, B_i, B_c \rightarrow B_{fc}, B_i, B_c \rightarrow A_f, B_i, A_f$	$4\alpha_B\gamma_A\gamma_B(p - \alpha_A)(1 - \alpha_B - p)$
$A_c, B_{nc}, B_{nc} \rightarrow B_{fc}, B_{nc}, B_{nc} \rightarrow A_f, B_{nc}, B_{nc}$	$\gamma_A(1 - \gamma_B)^2(p - \alpha_A)(1 - \alpha_B - p)^2$
$A_c, B_{nc}, B_c \rightarrow B_{fc}, B_{nc}, B_c \rightarrow A_f, B_{nc}, A_f$	$4\gamma_A\gamma_B(1 - \gamma_B)(p - \alpha_A)(1 - \alpha_B - p)^2$
$A_c, B_c, B_c \rightarrow B_{fc}, B_c, B_c \rightarrow A_f, A_f, A_f$	$3\gamma_A\gamma_B^2(p - \alpha_A)(1 - \alpha_B - p)^2$
$B_i, B_i, B_i \rightarrow B_i, B_i, B_i$	0
$B_i, B_i, B_{nc} \rightarrow B_i, B_i, B_{nc}$	0
$B_i, B_i, B_c \rightarrow B_i, B_i, B_c \rightarrow B_i, B_i, A_f$	$\alpha_B^2\gamma_B(1 - \alpha_B - p)$
$B_i, B_{nc}, B_{nc} \rightarrow B_i, B_{nc}, B_{nc}$	0
$B_i, B_{nc}, B_c \rightarrow B_i, B_{nc}, B_c \rightarrow B_i, B_{nc}, A_f$	$2\alpha_B\gamma_B(1 - \gamma_B)(1 - \alpha_B - p)^2$
$B_i, B_c, B_c \rightarrow B_i, B_c, B_c \rightarrow B_i, A_f, A_f$	$2\alpha_B\gamma_B^2(1 - \alpha_B - p)^2$
$B_{nc}, B_{nc}, B_{nc} \rightarrow B_{nc}, B_{nc}, B_{nc}$	0
$B_{nc}, B_{nc}, B_c \rightarrow B_{nc}, B_{nc}, B_c \rightarrow B_{nc}, B_{nc}, A_f$	$\gamma_B(1 - \gamma_B)^2(1 - \alpha_B - p)^3$
$B_{nc}, B_c, B_c \rightarrow B_{nc}, B_c, B_c \rightarrow B_{nc}, A_f, A_f$	$2(1 - \gamma_B)\gamma_B^2(1 - \alpha_B - p)^3$
$B_c, B_c, B_c \rightarrow B_c, B_c, B_c \rightarrow A_f, A_f, A_f$	$\gamma_B^3(1 - \alpha_B - p)^3$

3.6.4  $L = 3$ : analysis for the fully symmetric case  $\alpha_A = \alpha_B$  and  $\gamma_A = \gamma_B$ 

The derivative (with respect to  $p$ )  $f'_{3;\alpha,\alpha;\gamma,\gamma}$  of the function  $f_{3;\alpha,\alpha;\gamma,\gamma}$  as given by expression (3.9) in the equilibrium  $\hat{p} = 0.5$  equals  $0.5(3 - 4\alpha)(1 - 2\gamma)$ . There are two additional equilibria

$$\hat{p}_{3;\alpha,\alpha;\gamma,\gamma} = 0.5 \frac{1 - 2\gamma \pm \sqrt{(1 - 2\gamma)(-2 + (3 - 4\alpha)(1 - 2\gamma))}}{1 - 2\gamma} \in [\alpha, 1 - \alpha] \quad (3.13)$$

if and only if  $0 \leq \gamma < \frac{1}{6}$  and  $0 < \frac{1-6\gamma}{1-2\gamma} - 4\alpha$ . If the two additional equilibria exist they are symmetrically positioned on opposite sides of 0.5, and asymptotically stable; the equilibrium 0.5 then is unstable, with  $f'_{3;\alpha,\alpha;\gamma,\gamma}(0.5) > 1$ .

For  $\alpha$  and  $\gamma$  such that  $\frac{5}{6} < \gamma \leq 1$  and  $0 < \frac{5-6\gamma}{1-2\gamma} - 4\alpha$ , the equilibrium 0.5 also is unstable, with  $f'_{3;\alpha,\alpha;\gamma,\gamma}(0.5) < -1$ . In this case the dynamics  $\overrightarrow{f_{3;\alpha,\alpha;\gamma,\gamma}}$  has two asymptotically stable periodic points  $p_{3;\alpha;\gamma}^*$  of minimal period 2, symmetrically positioned with respect to 0.5:

$$p_{3;\alpha,\alpha;\gamma,\gamma}^* = 0.5 \frac{1 - 2\gamma \pm \sqrt{(1 - 2\gamma)(2 + (3 - 4\alpha)(1 - 2\gamma))}}{1 - 2\gamma} \in [\alpha, 1 - \alpha]. \quad (3.14)$$

3.6.5  $L = 3$ : analysis of the general case

The possible equilibria for  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}}$  (in  $[\alpha_A, 1 - \alpha_B]$ ) follow from solving  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) = p$ , under the restriction that  $p \in [\alpha_A, 1 - \alpha_B]$ . We distinguish several cases.

1.  $(\gamma_A, \gamma_B) = (0.5, 0.5)$ : expression (3.8) equals  $f_{3;\alpha_A,\alpha_B;0.5,0.5}(p) = 0.5(1 + \alpha_A - \alpha_B)$ , and allows for a unique stable equilibrium  $\hat{p} = 0.5(1 + \alpha_A - \alpha_B)$ , on which opinion  $A$  has the majority if and only if  $\alpha_A > \alpha_B$ .
2.  $(\gamma_A, \gamma_B) \neq (0.5, 0.5)$ ,  $\gamma_A + \gamma_B = 1$ : the function  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}$  is quadratic in  $p$ . The discriminant  $D(\alpha_A, \alpha_B; \gamma_A, \gamma_B)$  for the equation  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) - p = 0$  equals  $4\alpha_B^2 + 4\gamma_A(1 - \alpha_A^2 - 3\alpha_B^2) - 4\gamma_A^2(1 - 2(\alpha_A^2 + \alpha_B^2))$ . The opinion dynamics  $\overrightarrow{f_{3;\alpha_A,\alpha_B;\gamma_A,1-\gamma_A}}$  has a unique equilibrium

$$\hat{p}_{3;\alpha_A,\alpha_B;\gamma_A,1-\gamma_A} = \frac{1 - \gamma_A + (1 - 2\gamma_A)\alpha_A - \sqrt{(1 - \gamma_A)(1 - 2\gamma_A)\alpha_B^2 + \gamma_A(1 - \gamma_A) - \gamma_A(1 - 2\gamma_A)\alpha_A^2}}{(1 - 2\gamma_A)(1 + \alpha_A + \alpha_B)} \quad (3.15)$$

in the interval  $[\alpha_A, 1 - \alpha_B]$ . The derivative in the equilibrium equals

$$1 - 2\sqrt{\gamma_A(1 - \gamma_A) + (1 - \gamma_A)(1 - 2\gamma_A)\alpha_B^2 - \gamma_A(1 - 2\gamma_A)\alpha_A^2}.$$

3.  $\gamma_A + \gamma_B \neq 1$ . The expression  $f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) - p = 0$  for determining the equilibria now is

$$\begin{aligned} f_{3;\alpha_A,\alpha_B;\gamma_A,\gamma_B}(p) - p = \\ \alpha_A(1 - \gamma_A) + (1 - \alpha_B)\gamma_B - (1 + 2\alpha_A(1 - 2\gamma_A) - \gamma_A + \gamma_B)p_t + \\ (3 + \alpha_A(1 - 2\gamma_A) - \alpha_B(1 - 2\gamma_B) - 4\gamma_A - 2\gamma_B)p_t^2 - 2(1 - \gamma_A - \gamma_B)p_t^3 = 0. \end{aligned} \quad (3.16)$$

Its discriminant is

$$D(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = \left(\frac{1}{2}q_1(\alpha_A, \alpha_B; \gamma_A, \gamma_B)\right)^2 + \left(\frac{1}{3}q_2(\alpha_A, \alpha_B; \gamma_A, \gamma_B)\right)^3,$$

with

$$c_0(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = \alpha_A(1 - \gamma_A) + (1 - \alpha_B)\gamma_B,$$

$$c_1(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = -(1 + 2\alpha_A(1 - 2\gamma_A) - \gamma_A + \gamma_B),$$

$$c_2(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = 3 + \alpha_A(1 - 2\gamma_A) - \alpha_B(1 - 2\gamma_B) - 4\gamma_A - 2\gamma_B,$$

$$c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = -2(1 - (\gamma_A + \gamma_B)),$$

and

$$\begin{aligned} q_1(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = \frac{2}{27} \left( \frac{c_2(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}{c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B)} \right)^3 - \\ \frac{1}{3} \frac{c_2(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}{c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B)} \frac{c_1(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}{c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B)} + \frac{c_0(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}{c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}, \end{aligned}$$

$$q_2(\alpha_A, \alpha_B; \gamma_A, \gamma_B) = -\frac{1}{3} \left( \frac{c_2(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}{c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B)} \right)^2 + \frac{c_1(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}{c_3(\alpha_A, \alpha_B; \gamma_A, \gamma_B)}.$$

Figure 3.6 shows a selection of sign plots of the discriminant for this case. In addition the results of the analysis for combinations  $(\alpha, \alpha; \gamma, \gamma)$  is included.



# **Part II**

## **Adaptive Dynamics**





## ON THE CONCEPT OF ATTRACTOR FOR COMMUNITY-DYNAMICAL PROCESSES: THE CASE OF UNSTRUCTURED POPULATIONS

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This chapter is based on:

F. J. A. Jacobs and J. A. J. Metz, On the concept of attractor for community-dynamical processes I: The case of unstructured populations, *Journal of Mathematical Biology* 47, 222-234, 2003

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### ABSTRACT

We introduce a notion of attractor adapted to dynamical processes as they are studied in community-ecological models and their computer simulations. This attractor concept is modeled after that of Ruelle as presented in [84] and [85]. It incorporates the fact that in an immigration-free community populations can go extinct at low values of their densities.

Keywords: Community dynamics, attractors, adaptive dynamics, chain recurrence, pseudo-orbits

MSC (2020): 37b20, 37c20, 37c70

### 4.1 INTRODUCTION

The aim of this paper is to introduce a modification of the attractor concept introduced by Ruelle ([84], [85]) and Hurley ([50]) (based on ideas of Conley ([13])), below referred to as chain attractors, that is adapted to the asymptotic behaviour

of the dynamical systems studied in community ecology. The construction of chain attractors is based on the idea that any mathematical system is but an idealisation of reality and that neither physical nor numerical experiments produce the precise orbits of the theoretical system under consideration, but rather so-called pseudo-orbits that occur as a consequence of small disturbances or roundoff errors. We opted for the name chain attractor to bring out the close connection of this attractor concept with the notion of chain recurrence. Below we shall give a short review of Ruelle's construction and some of its properties (Section 2). In addition we introduce the useful terms chain repeller and chain saddle, and basin of chainability and of chain attraction, as it is sometimes convenient to refer to these concepts by name. Next we propose the modification (Section 3), followed by four examples (Section 4) and a discussion (Section 5). This modification is necessary in order to deal with the feature of extinction of a population as it may occur in community dynamics: a pseudo-orbit that reaches a boundary plane of the community state space spanned by the densities of the populations involved, will proceed in this boundary plane and cannot enter again into the interior of the community state space. This condition is not imposed in the construction of ordinary chain attractors, which in essence have their motivation in physics rather than community ecology.

#### 4.2 CHAINING, CHAIN ATTRACTORS AND BASIN OF CHAIN ATTRACTION

No model of an empirical process in the form of a smooth deterministic dynamical system is ever exact. At best the empirical process matches its theoretical model up to some continual small perturbations of its states (due to externally imposed or internally generated noise in the case of physical, chemical or biological processes, or cut-off errors in the case of numerical processes). One way of formalising the ubiquitous presence of small perturbations is in terms of pseudo-orbits, to be defined below, leading to a characterisation of their asymptotic behaviour by means of chain attractors, which are constructed in terms of these pseudo-orbits. In this section we summarise this construction as presented in [84] and Section 8 of [85]. We concentrate on those results that are of importance with regard to the

modification that we propose in the next section; for a more extensive exposition of the various concepts the reader is referred to [1].

Let  $(M, d)$  be a compact metric space, and let  $(\phi^t)_{t \geq 0}$  be a continuous semiflow on  $M$ . Furthermore, let  $\varepsilon > 0$  and let  $t_0, t_1 \in \mathbb{R}$ , with  $t_0 \leq t_1$ . An  $\varepsilon$ -pseudo-orbit  $\eta_{\varepsilon, [t_0, t_1]}$  of  $(\phi^t)_{t \geq 0}$  is a (not necessarily continuous) function  $\eta_{\varepsilon, [t_0, t_1]} : [t_0, t_1] \rightarrow M$  such that

$$d\left(\phi^\beta(\eta_{\varepsilon, [t_0, t_1]}(t + \alpha)), \phi^{\alpha+\beta}(\eta_{\varepsilon, [t_0, t_1]}(t))\right) < \varepsilon$$

whenever  $\alpha, \beta \geq 0$ ,  $\alpha + \beta \leq 1$ , and  $t, t + \alpha \in [t_0, t_1]$ . Thus, during a unit time  $\varepsilon$ -pseudo-orbits are allowed to "accrue an amount of error of at most  $\varepsilon$  relative to orbits", where the error measure takes into account how the error is transported along orbits (see Figure 1). (Another way of looking at  $\varepsilon$ -pseudo-orbits is by noting that in whatever way we sample the error within time steps  $\leq 1$ , the error per step relative to the unperturbed orbit will always be smaller than  $\varepsilon$ .)

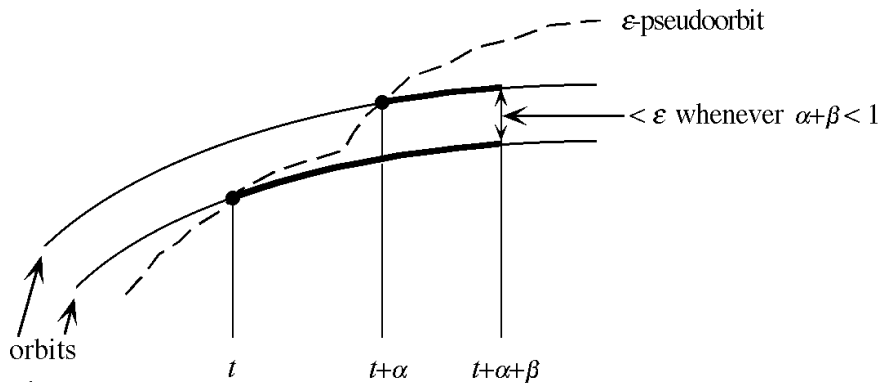


Figure 4.1: An illustration of an  $\varepsilon$ -pseudo-orbit

An  $\varepsilon$ -pseudo-orbit  $\eta_{\varepsilon, [t_0, t_1]}$  is said to go from  $\eta_{\varepsilon, [t_0, t_1]}(t_0)$  to  $\eta_{\varepsilon, [t_0, t_1]}(t_1)$  (or to start in  $\eta_{\varepsilon, [t_0, t_1]}(t_0)$  and to end in  $\eta_{\varepsilon, [t_0, t_1]}(t_1)$ ), and to have length  $t_1 - t_0$ . (Note that the word "length" is used here in an unusual, but time honoured, manner for the time taken instead of the traversed distance.) By concatenation of two  $\varepsilon$ -pseudo-orbits, one going from  $x$  to  $y$  and of length  $T$ , the second one going from  $y$  to  $z$  and of length  $T'$ , we obtain a  $2\varepsilon$ -pseudo-orbit going from  $x$  to  $z$  and of length  $T + T'$ . The deviation from an unperturbed orbit allowed for in  $\varepsilon$ -pseudo-orbits is controlled in time by the bound imposed on the sum  $\alpha + \beta$ , and in state space by  $\varepsilon$ , where a change in one can be compensated by an appropriate change in the other.

For the applications of  $\varepsilon$ -pseudo-orbits we have in mind in this paper only arbitrarily small values of  $\varepsilon$  are of importance.

Under the dynamical system  $(\phi^t)_{t \geq 0}$  on  $M$  the possible future states of an arbitrary  $x \in M$  are well-determined by its forward orbit  $\{\phi^t(x)\}_{t \geq 0}$ . As indicated above, an  $\varepsilon$ -pseudo-orbit (more precisely, its image) through  $x$  may deviate from this forward orbit. The intersection  $C_+(x) = \bigcap_{\varepsilon > 0} N_{\varepsilon,+}(x)$ , with  $N_{\varepsilon,+}(x)$  the union of the images of all  $\varepsilon$ -pseudo-orbits of  $(\phi^t)_{t \geq 0}$  starting at  $x$ , is called the *forward chain lineage through  $x$* . The forward orbit through  $x$  is contained in the forward chain lineage through  $x$ . However, where an orbit through  $x$  'ends' in the  $\omega$ -limit set of  $x$ , the forward chain lineage through  $x$  may proceed beyond this  $\omega$ -limit set. For example, the forward chain lineage through an  $x$  on the stable manifold of a saddle-point contains in addition to the orbit through  $x$  at least also the full unstable manifold of that saddle-point. Analogously we can introduce the *backward chain lineage through  $x$* ,  $C_-(x)$ , as the union of the images of all  $\varepsilon$ -pseudo-orbits of  $(\phi^t)_{t \geq 0}$  ending at  $x$ ; the union  $C(x) = C_+(x) \cup C_-(x)$  then is the *chain lineage through  $x$* .

A point  $x$  is chain recurrent if for every  $\varepsilon > 0$  and every  $T > 0$ , there is an  $\varepsilon$ -pseudo-orbit of length  $\geq T$  going from  $x$  to  $x$ . Chain recurrence captures the notion of positive recurrence under arbitrarily small perturbations. (We recall that an element  $x \in M$  is positively recurrent (in the ordinary sense) if for each  $\delta > 0$  and each  $T > 0$  there exists a  $t > T$  such that  $d(\phi^t(x), x) < \delta$ .) The set of chain recurrent points is the chain recurrent set. Points that are not chain recurrent we shall refer to as *ephemeral*.

On  $M$  the following relation  $\succcurlyeq$ , to be called *chaining*, is defined:  $x \succcurlyeq y$  (' $x$  chains to  $y$ ') if for every  $\varepsilon > 0$  there exists an  $\varepsilon$ -pseudo-orbit going from  $x$  to  $y$ . (Roughly stated  $x \succcurlyeq y$  means that there is an orbit or an arbitrarily little perturbed orbit, or a sequence of arbitrarily little perturbed orbits, in  $M$  going from  $x$  to  $y$ .) Note that the forward chain lineage through  $x$  corresponds to the image of  $x$  under the relation  $\succcurlyeq$ . The relation  $\succcurlyeq$  is reflexive ( $x \succcurlyeq x$ , trivially by means of an  $\varepsilon$ -pseudo-orbit of length 0) and transitive ( $x \succcurlyeq y$  and  $y \succcurlyeq z$  imply  $x \succcurlyeq z$ ), and thus is a preorder on  $M$ . The relation  $\succcurlyeq$  is also closed, in the sense that if  $(x_i)$  and  $(y_i)$  are two sequences in  $M$  converging to  $x$  and  $y$  respectively and such that for all  $i$ :  $x_i \succcurlyeq y_i$ , then  $x \succcurlyeq y$ .

(For a proof of this statement see [1], Chapter 1 Proposition 8.) As a consequence, the chain recurrent set is closed. The following Proposition is straightforward (see also [1], Chapter 1 Proposition 11):

**Proposition 1.** Let  $x, y \in M$ .  $x \succcurlyeq y$  if and only if either there is a  $t \geq 0$  such that  $\phi^t(x) = y$  or for all  $t \geq 0$ :  $\phi^t(x) \succcurlyeq y$ .

On  $M$  the relation  $\sim$ , to be called *mutual chaining*, is defined in the following way:  $x \sim y$  (' $x$  and  $y$  chain to each other') if  $x \succcurlyeq y$  and  $y \succcurlyeq x$ . Since  $\succcurlyeq$  is a preorder,  $\sim$  is an equivalence relation on  $M$ . The equivalence class of  $x$  under  $\sim$  is denoted by  $[x]$ . Clearly  $\sim$  is a closed relation (in the sense indicated above), and therefore every equivalence class is closed.

An equivalence class  $[x]$  is called a basic class if  $x$  (and consequently every  $y \in [x]$ ) is chain recurrent, and the chain recurrent set then is the union of all basic classes.

**Proposition 2.** The following three statements are equivalent:

1.  $[x]$  is a basic class;
2.  $x$  is a fixed point or  $[x]$  contains more than one point;
3. for all  $t \geq 0$ :  $\phi^t([x]) = [x]$ .

The proof of this Proposition follows from Proposition 1.

A class that is not basic, as well as the corresponding state, will be called *chain ephemeral*.

Let  $\mathcal{M} = \{[x] | x \in M\}$  denote the set of equivalence classes in  $M$  under  $\sim$ . On  $\mathcal{M}$  the relation  $\succcurlyeq$ , to be called *connecting*, is defined by:  $[x] \succcurlyeq [y]$  (' $[x]$  connects to  $[y]$ ') if  $x \succcurlyeq y$ . This relation is reflexive and transitive. In addition,  $[x] \succcurlyeq [y]$  and  $[y] \succcurlyeq [x]$  together imply that  $[x] = [y]$ . The relation  $\succcurlyeq$  thus imposes a partial ordering on  $\mathcal{M}$ .

**Definition 1.** A minimal element in  $\mathcal{M}$  under  $\succcurlyeq$  is called a chain attractor.

An existence proof, through the use of Zorn's lemma, can be found in [84].

Ruelle in [84] and [85] does not introduce any special term to characterise his attractors; Buescu in [4] uses the term Conley-Ruelle attractor. Hurley, who

independently introduced the same concept in [50] (though through a different, less physically interpretable, construction) refers to it as chain transitive quasi-attractor. Neither term seems to have caught on yet.

A chain attractor is a basic class, and, by Proposition 2, contains the  $\omega$ -limit sets of all its elements.

In addition to the above review of the idea of chain attractor, we introduce the terms chain repeller and chain saddle, and basin of chainability and basin of chain attraction.

**Definition 2.**

- (i) A maximal basic class in  $\mathcal{M}$  under  $\succcurlyeq$  is called a chain repeller.
- (ii) Any basic class in  $\mathcal{M}$  which is neither minimal nor maximal under  $\succcurlyeq$  is called a chain saddle.
- (iii) Chain ephemeral classes, chain repellers and chain saddles, c.q. the states therein, shall be referred to as chain transient.

If  $M$  is a manifold with boundary, any ephemeral maximal class in  $\mathcal{M}$  under  $\succcurlyeq$  necessarily is contained in the boundary of  $M$ . This follows easily from the fact that an orbit through an ephemeral state in the interior of  $M$  can be extended backward in time to another ephemeral state in the interior.

**Definition 3.** Let  $x \in M$ .

- (i) The basin of chainability of  $x$ , denoted  $B_{\succcurlyeq}(x)$ , is the collection of points  $y \in M$  that chain to  $x$ :  $B_{\succcurlyeq}(x) = \{y \in M | y \succcurlyeq x\}$ .
- (ii) The basin of chainability of the equivalence class  $[x]$ , denoted  $B_{\succcurlyeq}([x])$ , is:  $B_{\succcurlyeq}([x]) = B_{\succcurlyeq}(x)$ .
- (iii) If  $[x]$  is a chain attractor, we refer to its basin of chainability as its basin of chain attraction, and shall denote it as  $Att([x])$ .

Note that for each  $x \in M$ ,  $B_{\succcurlyeq}(x) \neq \emptyset$  since  $x \in B_{\succcurlyeq}(x)$ . An element of  $M$  can belong to several basins of chainability, and each element of  $M$  belongs to the basin of chain attraction of at least one chain attractor (again by Zorn's lemma, see [84]).

Therefore the different asymptotic regimes of a dynamical system, described by a semiflow on  $M$  that is subject to (very) small perturbations, are captured by its chain attractors.

#### 4.3 EXTINCTION PRESERVING CHAIN ATTRACTORS FOR IMMIGRATION-FREE COMMUNITIES

We now restrict our attention to point-dissipative community-dynamical processes for closed communities (i.e., communities without immigration). We recall that a dynamical system is point-dissipative if there exists a bounded set such that each orbit eventually enters this set and remains in it. The compact metric space  $(M, d)$  of the previous section here is understood to be the community state space spanned by the densities of the populations involved in the community-dynamical process under consideration. For  $k \geq 1$  populations  $1, \dots, k$ , with respective densities  $n_1, \dots, n_k$ ,  $M$  is the intersection of  $\mathbb{R}_+^k \subset \mathbb{R}^k$  with the closure of a simply connected neighbourhood of  $o$  in  $\mathbb{R}^k$ .  $M$  is supposed to be provided with the standard (Euclidean) metric and topology.

For  $l \in \mathbb{N}$ , with  $1 \leq l \leq k$ , and for  $i_1, \dots, i_l \in \{1, \dots, k\}$  such that  $1 \leq i_1 < \dots < i_l \leq k$ ,  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$  denotes the set

$$\left\{ (n_1, \dots, n_k) \in \mathbb{R}_+^k \mid n_{i_1} = \dots = n_{i_l} = 0 \right\} \subset \text{bd}(\mathbb{R}_+^k) = \left\{ (n_1, \dots, n_k) \in \mathbb{R}_+^k \mid \exists i \in \{1, \dots, k\} : n_i = 0 \right\},$$

which is the boundary set of  $\mathbb{R}_+^k$ . Furthermore we write  $\text{bd}_{i_1, \dots, i_l}(M)$  for  $M \cap \text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$ , and call it the extinction boundary for the populations  $i_1, \dots, i_l$ ;  $\text{bd}_e(M)$  denotes the intersection of  $M$  with  $\text{bd}(\mathbb{R}_+^k)$ . In addition, we write  $\text{bd}_{\text{int}}(M)$  for the intersection of the boundary of  $M$  with  $\text{int}(\mathbb{R}_+^k)$ . The assumption of no immigration translates into the invariance of the extinction boundaries  $\text{bd}_{i_1, \dots, i_l}(M)$  under the semiflow  $(\phi^t)_{t \geq 0}$ .

For later use we mention here that  $M$  is a normal space, i.e., it satisfies the following property: if  $C_1$  and  $C_2$  are two closed and disjoint subsets of  $M$ , then there exist open and disjoint subsets  $O_1, O_2$  in  $M$  such that  $C_1 \subset O_1$  and  $C_2 \subset O_2$ .

The closure of a subset  $U$  of  $M$  will be denoted by  $\bar{U}$ .

For  $n \in \text{bd}_{i_1, \dots, i_l}(M)$  the equivalence class generated by the relation of mutual chaining connected to the semiflow  $(\phi^t|_{\text{bd}_{i_1, \dots, i_l}(M)})_{t \geq 0}$  will be denoted as  $[n]_{i_1, \dots, i_l}$ .

In the theory reviewed in Section 2, an  $\varepsilon$ -pseudo-orbit which has a point in common with (or, more generally, comes arbitrarily close to) an extinction boundary of  $M$ , may again get away from this extinction boundary and proceed in  $M \setminus \text{bd}_e(M)$ . This is unrealistic in the case of community-dynamical processes, in which populations that attain densities arbitrarily close to zero are bound to go irreversibly extinct due to the discreteness of individuals. To incorporate this restriction into our considerations we introduce the notion of extinction preserving  $\varepsilon$ -pseudo-orbits.

**Definition 4.** Let  $\eta_{\varepsilon, [t_0, t_1]}$  be an  $\varepsilon$ -pseudo-orbit in  $M$ . For  $t_\alpha \in [t_0, t_1]$ ,  $\text{ext}(t_\alpha)$  denotes the collection of the minimal (with regard to the partial ordering by  $\subseteq$ ) extinction boundaries that have a non-empty intersection with the set of accumulation points  $\lim_{t \rightarrow t_\alpha} \eta_{\varepsilon, [t_0, t_1]}(t)$ .

Note that if  $\eta_{\varepsilon, [t_0, t_1]}$  is (left-)continuous in  $t = t_\alpha$ , then  $\text{ext}(t_\alpha)$  contains only the unique minimal extinction boundary containing  $\eta_{\varepsilon, [t_0, t_1]}(t_\alpha)$ .

**Definition 5.** An  $\varepsilon$ -pseudo-orbit  $\eta_{\varepsilon, [t_0, t_1]}$  in  $M$  is extinction preserving (abbreviated as ep) if the following property holds: if  $t_\alpha \in [t_0, t_1]$  is such that  $\text{ext}(t_\alpha) \neq \emptyset$ , then there is a  $\text{bd}_{i_1, \dots, i_l}(M) \in \text{ext}(t_\alpha)$  such that for all  $t \in [t_\alpha, t_1]$ :  $\eta_{\varepsilon, [t_0, t_1]}(t) \in \text{bd}_{i_1, \dots, i_l}(M)$ .

In addition we define:

**Definition 6.** A point  $n$  is ep-chain recurrent if for every  $\varepsilon > 0$  and every  $T > 0$  there is an ep  $\varepsilon$ -pseudo-orbit of length  $\geq T$  going from  $n$  to  $n$ . The set of ep-chain recurrent points is called the ep-chain recurrent set.

Note that an ep-chain recurrent point satisfies either one of the following two mutually exclusive conditions:

1.  $n$  as well as every ep  $\varepsilon$ -pseudo-orbit going from  $n$  to  $n$  belongs to  $M \cap \text{int}(\mathbb{R}_+^k)$ ;
2.  $n$  as well as every ep  $\varepsilon$ -pseudo-orbit going from  $n$  to  $n$  belongs to  $M \cap \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ , for a unique  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$ .



Furthermore, the ep-chain recurrent set is a subset of the chain recurrent set.

In accordance with the previous section we define an equivalence relation on  $M$  and a partial ordering on the corresponding equivalence classes, now however in terms of ep  $\varepsilon$ -pseudo-orbits.

**Definition 7.** For  $a, b \in M$  we define  $a \succ_{ep} b$  (' $a$  ep-chains to  $b$ ') if for every  $\varepsilon > 0$  there exists an ep  $\varepsilon$ -pseudo-orbit going from  $a$  to  $b$ .

The relation  $\succ_{ep}$  (to be called *ep-chaining*) is a preorder on  $M$ . Ep-chaining is not necessarily a closed relation: if  $(a_i)$  and  $(b_i)$  are two sequences in  $M$  that converge to  $a$  and  $b$  respectively and are such that for all  $i$ :  $a_i \succ_{ep} b_i$ , then not necessarily  $a \succ_{ep} b$  (take e.g.  $a$  and  $b$  in different extinction boundaries of  $M$  and not in their intersection).

We shall refer to the image of  $a$  under  $\succ_{ep}$  as the forward ep-chain lineage through  $a$ , denoted as  $C_{ep,+}(a)$ . The backward ep-chain lineage through  $a$ , denoted as  $C_{ep,-}(a)$ , is defined as the inverse image of  $a$  under  $\succ_{ep}$ ; the ep-chain lineage through  $a$  is the union  $C_{ep,-}(a) \cup C_{ep,+}(a)$  and is denoted by  $C_{ep}(a)$ .

**Definition 8.** For elements  $a, b \in M$  the relation  $\sim_{ep}$  is defined by:  $a \sim_{ep} b$  if  $a \succ_{ep} b$  and  $b \succ_{ep} a$ .

Since  $\succ_{ep}$  is a preorder,  $\sim_{ep}$  is an equivalence relation on  $M$ , to be called *mutual ep-chaining*. The expression  $a \sim_{ep} b$  (' $a$  and  $b$  ep-chain to each other') implies that either both  $a$  and  $b$  belong to  $M \cap \text{int}(\mathbb{R}_+^k)$ , or that  $a$  and  $b$  both belong to  $M \cap \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ , for one and the same  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$ . The equivalence class of  $a$  under  $\sim_{ep}$  is denoted as  $[a]_{ep}$ , and  $\mathcal{M}_{ep}$  denotes the set of equivalence classes in  $M$  under  $\sim_{ep}$ . Note that the relation  $\sim_{ep}$  is not closed (in the sense indicated above).

**Proposition 3.** If  $\overline{[a]_{ep}} \subset M \cap \text{int}(\mathbb{R}_+^k)$ , then  $[a]_{ep} = [a]$ ; if  $\overline{[a]_{ep}} \subset M \cap \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ , then  $[a]_{ep} = [a]_{i_1, \dots, i_l}$ . Consequently, in both cases  $[a]_{ep}$  is closed.

**Proof**  $M$  is a normal space, and so are the  $\text{bd}_{i_1, \dots, i_l}(M)$ . Therefore, under the constraints of the Proposition, if  $b \in [a]_{ep}$  there exists a  $\delta > 0$  such that for every  $\varepsilon < \delta$  there exists at least one  $\varepsilon$ -pseudo-orbit going from  $a$  to  $b$  (and also at least one going from  $b$  to  $a$ ) that is confined to  $M \cap \text{int}(\mathbb{R}_+^k)$  or to  $M \cap \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ . Any of these  $\varepsilon$ -pseudo-orbits then are ep  $\varepsilon$ -pseudo-orbits.

**Definition 9.**  $[a]_{ep}$  is called an ep-basic class if  $a$  (and consequently every  $x \in [a]_{ep}$ ) is ep-chain recurrent.

The ep-chain recurrent set is the union of all ep-basic classes. Three equivalent statements similar to the characterisation of basic classes in Proposition 2 can be made for ep-basic classes:

**Proposition 4.** The following three statements are equivalent:

1.  $[a]_{ep}$  is an ep-basic class;
2.  $a$  is a fixed point or  $[a]_{ep}$  contains more than one point;
3. for all  $t \geq 0$ :  $\phi^t([a]_{ep}) = [a]_{ep}$ .

A class that is not ep-basic, as well as the corresponding state, will be called *ep-chain ephemeral*. As the term ephemeral is tied in the negative to the notion of recurrence, we have from the implications:

$$a \text{ is positively recurrent} \Rightarrow a \text{ is ep-chain recurrent} \Rightarrow a \text{ is chain recurrent}$$

that:

$$a \text{ is chain ephemeral} \Rightarrow a \text{ is ep-chain ephemeral} \Rightarrow a \text{ is ephemeral.}$$

**Definition 10.** For elements  $[a]_{ep}, [b]_{ep} \in \mathcal{M}_{ep}$  the relation  $\geq_{ep}$  is defined by:  $[a]_{ep} \geq_{ep} [b]_{ep}$  if  $a \succ_{ep} b$ .

The relation  $\geq_{ep}$  (to be called *ep-connecting*) is a partial ordering on the set of equivalence classes of  $\sim_{ep}$ . By means of  $\geq_{ep}$  we adapt the definitions of chain attractors, -repellers and -saddles to community-dynamical processes.

**Definition 11.**

- (i)  $[a]_{ep}$  is an ep-chain attractor if it is a minimal element of the partial ordering  $\geq_{ep}$ .
- (ii)  $[a]_{ep}$  is an ep-chain repeller if it is a maximal ep-basic class of the partial ordering  $\geq_{ep}$ .

- (iii)  $[a]_{ep}$  is an ep-chain saddle if it is an ep-basic class that is neither minimal nor maximal under  $\succ_{ep}$ .
- (iv) Ep-chain ephemeral classes, ep-chain repellers and ep-chain saddles, c.q. the states therein, shall be referred to as ep-chain transient.

An ep-chain attractor is an ep-basic class, and, by Proposition 4, contains the  $\omega$ -limit sets of all its elements.

Existence of ep-chain attractors follows along the same line of reasoning that guarantees the existence of chain attractors: since  $M$  is a normal space, under the restriction of ep  $\varepsilon$ -pseudo-orbits any forward ep-chain lineage necessarily ends up in either some compact set in the interior of the community state space, or in a compact set in the interior of one of the extinction boundaries, of which there are only finitely many. Since on such a compact set the restriction of  $\succ_{ep}$  coincides with  $\succ$ , we can fall back on Ruelle's result in [84] for chain attractors.

Any ephemeral maximal class in  $\mathcal{M}_{ep}$  under  $\succ_{ep}$  belongs to  $\overline{\text{bd}_{\text{int}}(M)}$ .

**Proposition 5.** Any ep-chain attractor is closed.

**Proof** If  $\text{not}(\overline{[a]_{ep}} \subset M \cap \text{int}(\mathbb{R}_+^k))$  or  $\overline{[a]_{ep}} \subset M \cap \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  for some  $i_1, \dots, i_l$ , then  $[a]_{ep}$  is not a minimal element of  $\succ_{ep}$ . The result now follows from Proposition 3.

In addition we adapt the definition of the basin of chainability.

**Definition 12.** Let  $a \in M$ .

- (i) The basin of ep-chainability of  $a$ , denoted  $B_{\succ_{ep}}(a)$ , is the collection of points  $b \in M$  that ep-chain to  $a$ :  $B_{\succ_{ep}}(a) = \{b \in M \mid b \succ_{ep} a\}$ .
- (ii) The basin of ep-chainability of the equivalence class  $[a]_{ep}$ , denoted  $B_{\succ_{ep}}([a]_{ep})$ , is:  $B_{\succ_{ep}}([a]_{ep}) = B_{\succ_{ep}}(a)$ .
- (iii) If  $[a]_{ep}$  is an ep-chain attractor, we refer to its basin of ep-chainability as its basin of ep-chain attraction, and shall denote it as  $\text{Att}_{ep}([a]_{ep})$ .

The basins of ep-chainability have properties similar to the ones for the basins of chainability: for each  $a \in M$ ,  $B_{\succ_{ep}}(a) \neq \emptyset$ ; also, an element of  $M$  can belong

to several basins of ep-chainability, and each element of  $M$  belongs to the basin of ep-chain attraction of at least one ep-chain attractor (by the same argument as used to show the existence of ep-chain attractors).

**Proposition 6.** Every chain attractor contains an ep-chain attractor.

**Proof** Let  $[a]$  denote a chain attractor. If  $[a] \subset M \cap \text{int}(\mathbb{R}_+^k)$  or  $[a] \subset M \cap \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ , then  $[a] = [a]_{ep}$  and the validity of the statement follows immediately. In general, choose  $b \in [a]$ .  $b$  belongs to the basin of ep-chain attraction of at least one ep-chain attractor  $[c]_{ep}$ . Since any ep  $\varepsilon$ -pseudo-orbit through  $b$  also is an  $\varepsilon$ -pseudo-orbit through  $c$ , it follows that  $[c]_{ep} \subset [a]$ .

#### 4.4 FOUR EXAMPLES

##### *Example 1*

Figure 4.2 depicts a dynamical system consisting of two populations that are population-dynamically equivalent, e.g. since their members differ only in some neutral marker. The dynamics is degenerate, in the sense that there exists a line AB of neutrally stable equilibria. Each equilibrium on this line attracts all points on the straight line through it and the origin, except for the origin itself (which is an unstable equilibrium on each line). In particular, A and B are globally stable equilibria for the two single populations.

For each pair  $E_1, E_2$  of neutrally stable equilibria on AB we have that  $E_1 \sim E_2$ , as  $E_1$  and  $E_2$  are connected for all  $\varepsilon > 0$  by back and forth  $\varepsilon$ -pseudo-orbits consisting of movement at a fixed speed  $\varepsilon/2$  along the line AB. Consequently, the line AB is the (unique) chain attractor for the dynamics depicted in Figure 4.2. The ep-chain attractors are given by equilibria A and B and the origin. The origin is a degenerate ep-chain attractor, since its basin of ep-chain attraction contains only one point (and it is at the same time an ep-chain repeller).

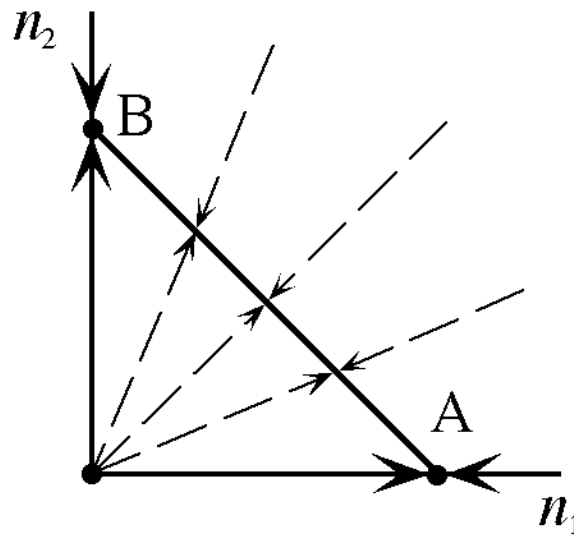


Figure 4.2: A degenerate dynamical system, which has the line AB as its unique chain attractor and A, B and the origin as its ep-chain attractors

### Example 2

The dynamical system depicted in Figure 4.3 results as the simplest perturbation of the degenerate case shown in Figure 4.2. The neutrally stable equilibria on AB in Figure 4.2 have turned ephemeral, but for the two single species and the one two-species equilibria. These three equilibria together with the origin are the ep-chain attractors.

### Example 3

In the May-Leonard system as described in [68], the community state moves towards a chain attractor in the form of a heteroclinic cycle in  $\text{bd}(\mathbb{R}_+^3)$ , connecting three single species equilibria; see Figure 4.4. These three equilibria and the origin are the ep-chain attractors of the system.

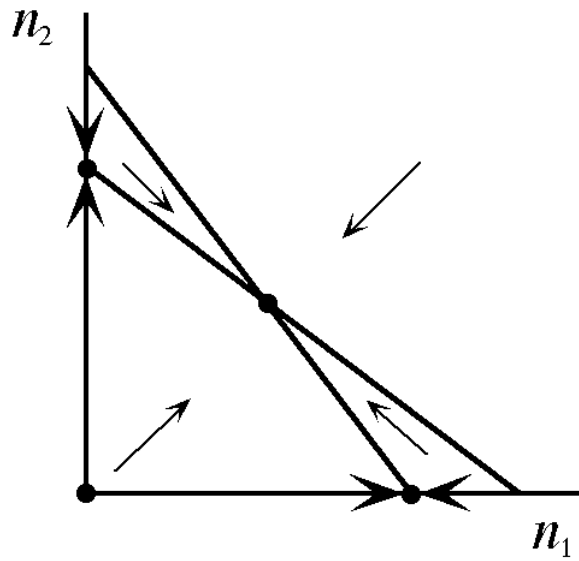


Figure 4.3: The simplest perturbation of the dynamical system from Example 1. The four ep-chain attractors are: the two-species equilibrium, the two non-trivial single species equilibria, and the origin

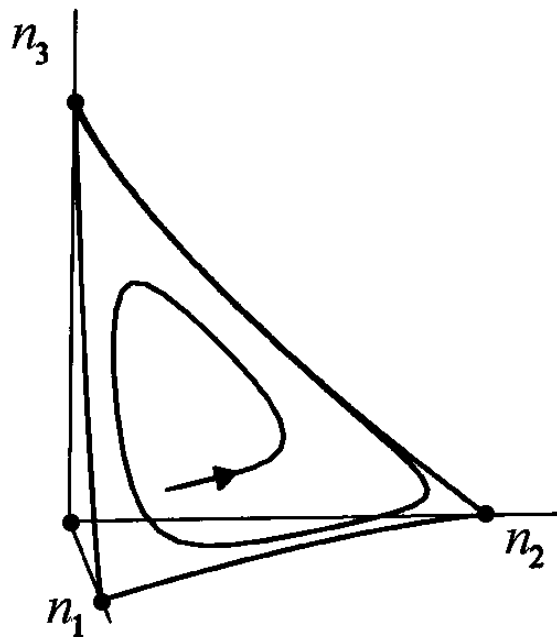


Figure 4.4: The May-Leonard dynamical system, with a heteroclinic cycle as its chain attractor and three non-trivial single species equilibria together with the origin as its ep-chain attractors

*Example 4*

This example illustrates that the ep-chain recurrent set does not necessarily have to be a closed set. In the dynamical system represented in Figure 4.5, a community in the interior of the community state space is attracted to a plane in whose interior the dynamics is determined by neutrally stable cycles. The ep-chain recurrent set consists of the interior of this plane together with three single species equilibria and the origin. Eventually any arbitrary community starting outside the origin will be confined to one of the three non-trivial ep-chain attractors of the system (the three non-trivial single species equilibria). The origin again is a degenerate ep-chain attractor.

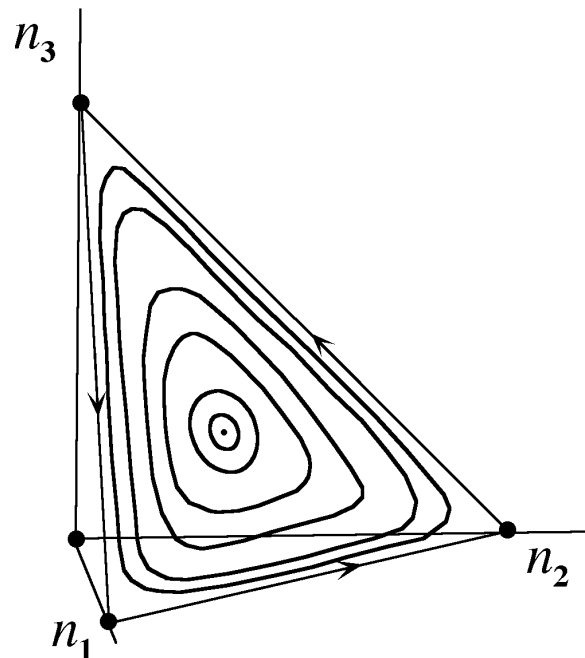


Figure 4.5: An example of a dynamical system with an open ep-chain recurrent set

## 4.5 DISCUSSION

We can expect that eventually the populations in a closed community-dynamical system will end up close to an ep-chain attractor in the interior of an  $\mathbb{R}_+^l$  (for an appropriate  $l \leq k$ , with  $k$  the number of populations

initially present in the community). The actual attractor that will be reached may depend on the perturbations that the community is exposed to.

A word of warning may be in order though: Along its way towards an (ep-) chain attractor, a community may pass through a cascade of (ep-)chain saddles to which it initially is attracted but from which it subsequently moves away. These phases each have their own specific timescale, measured by a relaxation and excitation time. Since these times can be considerably larger than the eventual relaxation time to the (ep-)chain attractor, it may in empirical practice sometimes be hard to decide whether or not a community is already approaching one of its (ep-)chain attractors.

A bifurcation theory for a class of community-dynamical systems  $(\phi_\mu^t)_{t \geq 0}$ , depending on a parameter (or a vector of parameters)  $\mu$ , in essence must study the relation between  $\mu$  and the induced ordering  $\geq_{ep}$  on  $\mathcal{M}_{ep}$ . The bifurcation points are those values of  $\mu$  for which in any neighbourhood there are parameter values for which  $\langle \mathcal{M}_{ep}, \geq_{ep} \rangle$  (i.e., the set  $\mathcal{M}_{ep}$  provided with the partial ordering relation  $\geq_{ep}$ ) belongs to a different order isomorphism class.

In the context of phenotypic trait evolution as studied in adaptive dynamics (e.g. [17], [39], [38], [73]), it is assumed that a mutant population emerges from a resident community on an attractor. This assumption is based on the notion that the time needed for a community to reach its attractor is shorter than the timespan between the occurrences of successful mutant populations (successful in the sense that a mutant population invades the resident community and increases its density, causing a change from residential community dynamics into a dynamics of the resident populations with the mutant population; as regards the justification of the assumption of timescale separation the proof of the pudding is in the eating.). However, it never was made very clear what was meant with an attractor. Basically the theory was developed only for systems having classical attractors with pretty strong properties, such as equilibria or limit cycles. The concept of ep-chain attractors provides one possible step towards a further extension of the reach of adaptive dynamics theory. In the special case of Lotka-Volterra community dynamics, it is more or less clear how one can build a theory starting from this attractor concept only (see [53]). In order to arrive at a well-structured theory of adaptive dynamics for more general types of community dynamics, at least some



restrictions will be necessary on the properties of the attractors that can occur. In any case, ep-chain attractors appear to be the minimal ingredients from which to start.



## ADAPTIVE DYNAMICS FOR LOTKA-VOLTERRA COMMUNITY DYNAMICS

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This chapter has not yet been published.

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### ABSTRACT

Adaptive dynamics considers phenotypic trait evolution as a process which proceeds in many successive small steps, each step being initiated by the occurrence of mutants in a community of resident populations. In this paper we analyse scalar phenotypic trait evolution in case the underlying community dynamics is given by a Lotka-Volterra model. The Lotka-Volterra model serves as a toy model to introduce several ideas of adaptive dynamics. These ideas go beyond the limitations of the Lotka-Volterra model under consideration; it is however only by simplifying that we can start to grasp the complex process of phenotypic trait evolution. The usual coefficients in the community-dynamical differential equations of the Lotka-Volterra model are obtained from two functions that have the phenotypic traits of the populations as their arguments. From the community-dynamical differential equations the invasion fitness function is derived. This function plays an essential role in adaptive dynamics. It expresses the initial fate of mutants after their emergence from the resident community in terms of the phenotypic trait values of both residents and mutants. The three processes that cause the change of the phenotypic composition of communities on the evolutionary timescale are trait substitution, evolutionary branching and evolutionary pruning, and these processes are analysed in terms of invasion fitness functions. Furthermore, we derive that for a large class of Lotka-Volterra models, permanence is maintained under sufficiently small mutational steps. We can represent trait evolution in a so-called Trait Evolution Plot, shortly denoted by

TEP. By making use of TEPs adaptive dynamics gets a geometric component, which can guide the intuition in finding patterns in the evolutionary process. Parts of our results also hold for adaptive dynamics of phenotypic trait vectors instead of scalar traits.

## 5.1 INTRODUCTION

Adaptive dynamics is a theory under construction which aims to describe in a mathematical way the biological phenomenon of phenotypic trait (or strategy) evolution. The theory relies heavily on the theory of dynamical systems as well as on the theory of stochastic processes (see e.g. the introductions [39], [38], [73]), which explains the manifold use of terminology from these fields of mathematics as well as of the relevant biological concepts. In this paper we shall not dwell on every facet of adaptive dynamics, but concentrate on the deterministic part of the theory.

Briefly one could say that adaptive dynamics considers phenotypic trait evolution as a process which proceeds in many successive small steps, each step being initiated by the occurrence of mutants in a community of resident populations. Each population consists of individuals that carry the same phenotypic trait value (or vector of trait values; in this paper we consider scalar traits, although several algebraic results also hold for trait vectors, as we shall indicate in the Discussion). We assume that there appears only one single mutant population at a time, emanated from one of the resident populations, an assumption justified by the general assumption of rareness of relevant mutations. The phenotypic trait values for resident and mutant populations are taken to be elements of a so-called *trait space*  $\mathbb{T}$ , which is a closed interval of the real numbers, and the mutants' phenotype is close to that of its progenitor population. The community-dynamical timescale is supposed to be much shorter than the evolutionary one. Therefore the resident community can be assumed to reside on a community-dynamical attractor, or *c*-attractor for short (the *c* here stems from community), in the interior of its community state space. This *c*-attractor is presumed to be "good", a characterisation which i.a. implies that it is a closed and bounded subset for which any potential mutant population has a uniquely associated transversal

Lyapunov exponent. Details of the notion of “good”  $c$ -attractor will be given in Section 5.2.4. A “good”  $c$ -attractor shall be represented by the traits of the resident populations that are present on it, and therefore can be taken to be an element of  $\mathbb{T}^k$  for an appropriate value of  $k$ . The adaptive-dynamical state space consists of the collection of possible  $c$ -attractors in the  $\mathbb{T}^k$ ,  $k \geq 1$ . A mutant population that emerges (evidently in very low density) from a resident  $c$ -attractor either will be successful or not in increasing its density. Unsuccessful mutants go extinct after a relatively short time (on the community-dynamical timescale) and leave the resident community on its  $c$ -attractor. Successful mutants invade the resident  $c$ -attractor. This initial fate of the mutant population depends on the mutants’ phenotype fitness on the attractor, which is captured by the invasion fitness function. Here fitness on a  $c$ -attractor is defined as the long-term averaged initial per capita growth rate (or transversal Lyapunov exponent, see [72]) of the mutant population in the environment set by that  $c$ -attractor, and as such is derived from the community-dynamical differential equations for the community of residents and mutants. (For general community-dynamical models there are some problems in selecting or even defining this Lyapunov exponent. However, all these problems conveniently disappear in a Lotka-Volterra community-dynamical context.) Mutants with traits that have a positive fitness on a  $c$ -attractor have a positive probability to invade that  $c$ -attractor, but will not always do so: due to the initially low density of the mutant population, invasion is a process on which demographic stochasticity has an essential influence. In an actual invasion process the mutant population may die out, despite its fitness being positive. A non-positive fitness translates into a zero probability of invasion by the mutants.

After invasion, the residents and mutants eventually home in on a (possibly unique)  $c$ -attractor in the community state space spanned by their population densities, or on a  $c$ -attractor in the community state space spanned by a subset of these densities. (Note that this addition with respect to a subset is necessary, since a  $c$ -attractor is assumed to lie in the interior of a community state space.) On this  $c$ -attractor the phenotypic composition of the community in general will be different from the one which became invaded. In case the mutant population replaces its progenitor population, we say that a *trait substitution* takes place (on the evolutionary timescale). A trait substitution leaves the number of populations

that constitute the community unaltered, and corresponds to a small change in the phenotypic trait composition of the community. The direction and size of this change are determined by the specific mutant population which by chance occurs and invades the resident  $c$ -attractor. The probability distribution for the mutant trait values that actually do invade is determined by the possible supply of mutants and by the probability that a given mutant population actually invades. This latter probability (which we assume to be a continuous function with respect to the mutants' trait value) is up to first order determined by the so-called *local fitness gradient* at the resident attractor as determined by the trait value of the population from which the mutants emerged. It thus follows that on a given  $c$ -attractor there exist as many local fitness gradients as there are resident populations present on that  $c$ -attractor.

If on the attractor approached by the residents and mutants all resident phenotypes together with the mutant trait are present, this  $c$ -attractor can be a steppingstone to so-called evolutionary branching. In the terminology of adaptive dynamics, *evolutionary branching* is an increase in the number of trait values which is enduring locally on the evolutionary timescale, i.e., it must persist at least long enough to be noticeable on that scale, even though in the long run an increase may disappear again due to so-called *evolutionary pruning* (see below). We shall derive that for a  $c$ -attractor to be a steppingstone to evolutionary branching, in general this  $c$ -attractor must be close to a  $c$ -attractor on which at least one of the local fitness gradients is equal to 0. In case invasion of the mutants causes the extinction of more than one of the populations in the community, there is a decrease in the number of phenotypes. A locally enduring decrease on the evolutionary timescale in the number of phenotypes is called evolutionary pruning. The terminology relates to the tree-like shapes that are obtained when the traits present on the  $c$ -attractors that are subsequently visited by the communities are plotted against evolutionary time. From the three possible scenarios after invasion of a mutant population, trait substitution will turn out to be the rule (pointwise in the adaptive-dynamical state space; evolutionary trajectories as a whole however may well branch or be pruned). By making use of these concepts, adaptive dynamics tries to give a gross dynamical explanation for changes in the phenotypic

composition of communities, in contrast to population dynamics where one is interested in the evolution in time of the densities of the constituent populations.

*c*-Attractors, fitness and the effect of an invasion are determined by the differential equations that describe the development in time of the densities of the interacting populations. These differential equations in turn depend on the phenotypic traits of the members of the community (and possibly on external environmental parameters). In this paper we study adaptive dynamics in case the community dynamics is given by a Lotka-Volterra model. For such models the invasion fitness functions and local fitness gradients can be calculated explicitly. The usual coefficients in the model, i.e., the per capita initial growth rates and the interaction coefficients, are derived from two functions that have the phenotypes of the involved populations as their variables. Necessary conditions for the possible outcomes for mutants and residents after invasion of the mutant population will be formulated, and it will turn out that these conditions can be stated solely in terms of invasion fitness functions. We shall determine when these conditions are being satisfied. We also show that for a large class of Lotka-Volterra models permanence is maintained under sufficiently small mutational steps. By means of a so-called Trait Evolution Plot (TEP) we can represent phenotypic trait evolution in a graphical way. Figure 2 shows an example of a TEP. By making use of TEPs adaptive dynamics gets a geometric component, which can guide the intuition in finding patterns in the evolutionary process. Furthermore the geometric aspect is appealing from a purely mathematical point of view.

Beside the presentation of the results of phenotypic trait evolution based on Lotka-Volterra community dynamics our aim is to whet the readers' appetite for adaptive dynamics as a theory that helps to understand the broad outlines of evolution. Lotka-Volterra-Based adaptive dynamics as discussed below therefore must be considered as a framework which serves to introduce several ideas of phenotype trait evolution that go beyond the limitations of the model under consideration (see also [73]). It is only by simplifying that we can come to grasp such a complex process as phenotype trait evolution, and can start to develop ingredients for a well-based theoretical framework. We present here pointers to some of those ingredients.

## 5.2 AN INTRODUCTION TO THE MATHEMATICAL FRAMEWORK

In this section we provide the basic tools and assumptions that are used in the mathematical description of scalar phenotypic trait evolution. The underlying community dynamics are taken to be those of Lotka-Volterra models. We shall use several properties of Lotka-Volterra models as they are derived in the standard reference [49].

## 5.2.1 Preliminaries on trait spaces and Lotka-Volterra community dynamics

We start with specifying the underlying Lotka-Volterra community dynamics and the role of phenotypic traits herein.

**Assumption 1.** Let a closed interval  $\mathbb{T} \subset \mathbb{R}$  be given, together with two bounded functions  $r : \mathbb{T} \rightarrow \mathbb{R}$  and  $a : \mathbb{T}^2 \rightarrow \mathbb{R}$ . The set  $\mathbb{T}$  will be called the trait space, and its elements are called trait values. The functions  $r$  and  $a$  are assumed to be as many times continuously differentiable as is required for our aims. For each  $k \in \mathbb{N}$ ,  $k \geq 1$ , and each  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  we define a Lotka-Volterra community-dynamical system for  $k$  populations, indicated by  $LV_k(\tau_1, \dots, \tau_k)$  and specified as follows:

1. In  $LV_k(\tau_1, \dots, \tau_k)$ , all individuals of population  $i \in \{1, \dots, k\}$  are being characterised by trait value  $\tau_i \in \mathbb{T}$ . The trait as represented by population  $i$  may also be called the  $i$ -trait value. The density of population  $i$  in  $LV_k(\tau_1, \dots, \tau_k)$  will be denoted by  $x_i$ <sup>1</sup>. The community state space spanned by the densities of the  $k$  populations is the nonnegative orthant

$$\mathbb{R}_+^k = \left\{ x = (x_1, \dots, x_k) \in \mathbb{R}^k \mid \text{for } i = 1, \dots, k : x_i \geq 0 \right\}.$$

For  $LV_k(\tau_1, \dots, \tau_k)$ , the densities develop in time according to the following set of differential equations on  $\mathbb{R}_+^k$ :

$$\frac{d}{dt}x_i = x_i \left( r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j)x_j \right), \quad i = 1, \dots, k. \quad (5.1)$$

<sup>1</sup> In this paper we adopt the notation for population density from [49].



The flow generated by equations (5.1) will be denoted by  $(x^t)$ , and  $(x^t)_{t \geq 0}$  denotes the induced semiflow. We shall refer to the function  $r$  as the initial per capita growth rate function, and to the function  $a$  as the interaction function for  $LV_k(\tau_1, \dots, \tau_k)$ . We assume that zeros of  $r$  (if they exist) are isolated.

For  $V \subset \mathbb{T}^k$ ,  $LV_k(V)$  denotes the family of Lotka-Volterra community-dynamical systems  $\{LV_k(\tau_1, \dots, \tau_k) | (\tau_1, \dots, \tau_k) \in V\}$ .

(Note that we do not require that two different populations  $i$  and  $j$  are characterised by different values  $\tau_i$  and  $\tau_j$ ; this allows us to split a population into two, a property which we shall introduce in subsection 5.2.2.)

2. The matrix  $A(\tau_1, \dots, \tau_k) = (a(\tau_i, \tau_j))_{1 \leq i, j \leq k}$  is called the interaction matrix for the system  $LV_k(\tau_1, \dots, \tau_k)$ .

With  $\tau$  denoting the vector  $(\tau_1, \dots, \tau_k)$ ,  $\mathbf{r}(\tau)$  the vector  $(r(\tau_1), \dots, r(\tau_k))$ , and  $\mathbf{x}$  the vector of densities  $(x_1, \dots, x_k)$ , the set of differential equations (5.1) may also be denoted as

$$\frac{d}{dt} \mathbf{x} = \mathbf{x} \circ (\mathbf{r}(\tau) + A(\tau_1, \dots, \tau_k) \mathbf{x}), \tag{5.2}$$

with  $\circ$  denoting the Hadamard product.

The determinant of  $A(\tau_1, \dots, \tau_k)$  shall be denoted by  $|A(\tau_1, \dots, \tau_k)|$ .

3. The function  $a$  is assumed to be such that for each function  $r$  and each choice of trait values  $\tau_1, \dots, \tau_k$ ,  $k \geq 1$ , the solutions of the Lotka-Volterra equations (5.1) are uniformly bounded for  $t \rightarrow +\infty$ . (The matrix  $A(\tau_1, \dots, \tau_k)$  then is called a  $B$ -matrix, see [49], and the uniformity holds with respect to initial conditions in  $\mathbb{R}_+^k$ ). Thus, given  $a$  and  $r$ , for each choice  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  there exists a (finite)  $b(r, a, \tau_1, \dots, \tau_k)$  such that for all  $x \in \mathbb{R}_+^k$  and all  $i \in \{1, \dots, k\}$ :
 
$$\limsup_{t \rightarrow +\infty} x_i(t) \leq b(r, a, \tau_1, \dots, \tau_k).$$
4. The community state spaces  $\mathbb{R}_+^k$  are provided with the sum norm, denoted by  $\|\cdot\|$ , and the metric, denoted by  $d$ , and topology induced by it. (Thus, for  $x = (x_1, \dots, x_k) \in \mathbb{R}_+^k$ ,  $\|x\| = \sum_{i=1}^k |x_i|$ , with in general  $|x|$  denoting the absolute value of the real number  $x$ .) The sets  $\mathbb{T}^k$  as well as any of their

subsets are assumed to be provided with the sup norm, denoted by  $\|\cdot\|_{sup}$ , and the metric and topology derived from it.

The elements of the trait space  $\mathbb{T}$  are numerical values of the manifestation of a (not further specified) metric (or scalar) phenotype. The  $\tau_i$ ,  $i = 1, \dots, k$ , in  $LV_k(\tau_1, \dots, \tau_k)$  are parameters for the community dynamics described by (5.1). Much of our concern deals with the effect that a small change in the phenotypic composition of a community, from  $(\tau_1, \dots, \tau_k)$  into  $(\tau_1, \dots, \tau_k, \nu)$ , has on its asymptotic dynamics. Here the  $\tau_i$ ,  $i = 1, \dots, k$ , denote the trait values of  $k$  resident populations, and  $\nu$  denotes the trait value of a mutant population that occurs in an infinitesimally small density. The value  $\nu$  is supposed to lie very close to  $\tau_i$ , for an  $i \in \{1, \dots, k\}$ . By identifying  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  with  $(\tau_1, \dots, \tau_k, \tau_i) \in \mathbb{T}^{k+1}$ , the change in phenotypic trait composition from  $(\tau_1, \dots, \tau_k, \tau_i)$  into  $(\tau_1, \dots, \tau_k, \nu)$  then indeed is small, in terms of the sup norm on  $\mathbb{T}^{k+1}$ . (The identification of  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  with  $(\tau_1, \dots, \tau_k, \tau_i) \in \mathbb{T}^{k+1}$  is common in adaptive dynamics, and is based on a notion of equivalence that will be introduced in the next subsection.) Note that we do not claim that the phenotypic change as caused by the occurrence of a mutant population is maintained throughout the asymptotic phase of the dynamics of the resident and mutant populations. The introduction of the mutants is the impetus for a dynamics whose outcome, in terms of phenotypic composition, may be different from the initial one. In fact, as we shall conclude, generically the values  $\tau_1, \dots, \tau_k, \nu$  that originally were present will not all be present in the end (on the community-dynamical timescale).

### 5.2.2 Trait-dependent ODE community-dynamical systems

The Lotka-Volterra systems  $LV_k(\tau_1, \dots, \tau_k)$  introduced above are special examples of trait-dependent ODE community-dynamical systems. These systems inherit a number of properties from the real processes they represent, which we discuss here in brief for later use.

In general, a trait-dependent ODE community-dynamical system for  $k$  populations is a dissipative system described by a collection of  $k$  differential equations

$$\frac{d}{dt}x_i = x_i f_k(x_1, \dots, x_k; \tau_1, \dots, \tau_k; \tau_i), i = 1, \dots, k, \quad (5.3)$$

with  $f_k : \mathbb{R}_+^k \times \mathbb{T}^k \times \mathbb{T} \rightarrow \mathbb{R}$  at least continuous. The first  $2k$  arguments of  $f_k$  represent again the  $k$  population densities respectively  $k$  trait values of the individuals of these populations; the last argument indicates the trait value of an arbitrary population that experiences the environment set by the densities of the populations and their trait values specified by the first  $2k$  arguments of  $f_k$  (and possibly by external environmental parameters that are left unspecified). We shall for the moment denote such a trait-dependent community-dynamical system simply by  $(\tau_1, \dots, \tau_k)$ . For the Lotka-Volterra system  $LV_k(\tau_1, \dots, \tau_k)$  the functions  $f_k$  are defined by

$$f_k(x_1, \dots, x_k; \tau_1, \dots, \tau_k; \tau) = r(\tau) + \sum_{i=1}^k a(\tau, \tau_i) x_i.$$

Based on ecological considerations, the functions  $f_k$  should in general have three properties that relate to the invariance of the community dynamics under a permutation of populations, the (absence of) effect on the community dynamics under the splitting of a population into two smaller subpopulations, and the invariance of the extinction subspaces  $x_i = 0, i = 1, \dots, k$  of the community state space. To formalise these properties we first introduce the following Notation.

**Notation 1.** Let  $k \geq 1$  in  $\mathbb{N}$  be given.

1.  $\Sigma_k$  denotes the set of permutations on  $k$  elements, and  $\sigma_0$  denotes the identity permutation in any  $\Sigma_k$ .
2.  $V_{k, \sigma_0}$  denotes the subset  $\{(\tau_1, \dots, \tau_k) \in \mathbb{T}^k \mid \tau_1 < \dots < \tau_k\}$  of  $\mathbb{T}^k$ . For  $\sigma \in \Sigma_k$ ,  $V_{k, \sigma}$  denotes the set  $\{(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}) \in \mathbb{T}^k \mid (\tau_1, \dots, \tau_k) \in V_{k, \sigma_0}\}$ .
3. Let  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$ , and for  $l \in \{1, \dots, k\}$  let  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  with  $i_1 < i_2 < \dots < i_l$ . Then  $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$  denotes the element  $(\tau_1, \dots, \tau_{i_1-1}, \tau_{i_1+1}, \dots, \tau_{i_l-1}, \tau_{i_l+1}, \dots, \tau_k) \in \mathbb{T}^{k-l}$ . In case the numbers  $i_1, \dots, i_l$  are not in increasing order,  $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$  denotes the

element  $(\tau_1, \dots, \tau_k \setminus \tau_{\sigma(i_1)}, \dots, \tau_{\sigma(i_l)})$ , with  $\sigma \in \Sigma_l$  the permutation that puts the sequence  $i_1, \dots, i_l$  in increasing order. In addition we introduce an element  $\lambda := (\tau_1, \dots, \tau_k \setminus \tau_1, \dots, \tau_k)$ , and set  $\mathbb{T}^0$  to be equal to  $\{\lambda\}$ .

4. Let  $i, j \in \{1, \dots, k\}$  with  $i < j$ . With  $\Delta_{i,j}^k$  we denote the diagonal hyperplane  $\tau_i = \tau_j$  of  $\mathbb{T}^k$ . The collection of all diagonal hyperplanes shall be denoted by  $\Delta^k = \bigcup_{1 \leq i < j \leq k} \Delta_{i,j}^k$ .

We now discuss the three ecological properties for trait-dependent community-dynamical systems (5.3) in more detail.

1. For all  $\sigma \in \Sigma_k$  and all  $\tau \in \mathbb{T}$ :

$$f_k(x_1, \dots, x_k; \tau_1, \dots, \tau_k; \tau) = f_k(x_{\sigma(1)}, \dots, x_{\sigma(k)}; \tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}; \tau).$$

This property states that the community dynamics of a community of  $k$  populations  $1, \dots, k$  is independent of the numbering of these populations. We shall call this property *exchangeability under permutation*, and we say that the systems  $(\tau_1, \dots, \tau_k)$  and  $(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)})$  are exchangeable under permutation.

2. For all  $(\tau_1, \dots, \tau_k) \in \Delta_{i,j}^k$  and  $\tau \in \mathbb{T}$ :

$$f_k(x_1, \dots, x_i, \dots, x_j, \dots, x_k; \tau_1, \dots, \tau_i, \dots, \tau_j, \dots, \tau_k; \tau) = f_{k-1}(x_1, \dots, x_i + x_j, \dots, x_{j-1}, x_{j+1}, \dots, x_k; \tau_1, \dots, \tau_i, \dots, \tau_{j-1}, \tau_{j+1}, \dots, \tau_k; \tau).$$

That is, if populations  $i$  and  $j$  are characterised by the same phenotypic trait value,  $\tau_i = \tau_j$ , the dynamics of the community is identical to that of a community of  $k - 1$  populations obtained by merging populations  $i$  and  $j$ . As a consequence, in the  $k$ -community the relative densities  $\frac{x_i(t)}{x_i(t) + x_j(t)}$  and  $\frac{x_j(t)}{x_i(t) + x_j(t)}$  are constant in time, their values being determined by their initial conditions. We shall refer to this property as *merging*, and we say that  $(\tau_1, \dots, \tau_k) \in \Delta_{i,j}^k$  merges to  $(\tau_1, \dots, \tau_k \setminus \tau_j)$ . Conversely this property allows, in a community of  $k$  populations, the splitting of a population  $i$  into two subpopulations characterised by the same phenotypic trait, without affecting the dynamics of the other populations. The dynamics of the sum of the

densities of the two subpopulations then is equal to that of population  $i$  in the original community, and the dynamics of the relative densities of the two subpopulations with regard to the density of the original population  $i$  is constant. This reversal of the merging property we shall call *splitting*, and we say that  $(\tau_1, \dots, \tau_i, \dots, \tau_k)$  splits into  $(\tau_1, \dots, \tau_i, \dots, \tau_k, \tau_i) \in \Delta_{i,k+1}^{k+1}$ .

3. For all  $\tau \in \mathbb{T}$  and all  $i \in 1, \dots, k$ :

$$f_k(x_1, \dots, x_{i-1}, 0, x_{i+1}, \dots, x_k; \tau_1, \dots, \tau_{i-1}, \tau_i, \tau_{i+1}, \dots, \tau_k; \tau) = f_{k-1}(x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_k; \tau_1, \dots, \tau_{i-1}, \tau_{i+1}, \dots, \tau_k; \tau).$$

This property states that on  $x_i = 0$  the community dynamics reduces to that obtained by removing population  $i$  from the community. In other words, a phenotypic trait value  $\tau_i$  is not allowed to affect the community if all its carriers are absent from that community. This property we shall call *reduction by absence*, and  $(\tau_1, \dots, \tau_k)$  is said to reduce to  $(\tau_1, \dots, \tau_k \setminus \tau_i)$  by absence of population  $i$ .

In correspondence to the properties of community-dynamical differential equations mentioned above we introduce the following notion of *phenotypic equivalence* of trait combinations (and their corresponding trait-dependent community-dynamical systems).

**Definition 1.**

1. Two elements  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  and  $(\tau'_1, \dots, \tau'_{k'}) \in \mathbb{T}^{k'}$  are phenotypically equivalent if there exists a composition of a permutation of indices and/or merging or splitting that maps either one of the trait combination onto the other one.
2. Two sets  $V \subset \mathbb{T}^k$  and  $V' \subset \mathbb{T}^{k'}$  are said to be phenotypically equivalent if each element of  $V$  is phenotypically equivalent to an element of  $V'$  and vice versa.

Phenotypic equivalence is an equivalence relation between trait combinations in  $\bigcup_{k \geq 1} \mathbb{T}^k$ . It allows us to introduce a notion of nearness of two trait combinations:

$(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  and  $(\tau'_1, \dots, \tau'_k) \in \mathbb{T}^k$  are near to each other if there is a composition of a permutation of indices and/or mergings or splittings under which the image of one of the trait combinations is close to the other trait combination. This notion of nearness will be exploited further in relation to trait evolution later on in the text.

**Remark 1.** Phenotypic equivalence of two community-dynamical systems does not imply their topological equivalence. To see this, consider a community-dynamical system  $(\tau)$  which has a non-trivial point-equilibrium.  $(\tau)$  clearly is phenotypically equivalent with  $(\tau, \tau)$ . However, since their community state spaces have different dimensions, there cannot exist a homeomorphism between the collections of orbits of the two systems.

### 5.2.3 Properties of the maps $\mathbb{T}^k \rightarrow LV_k(\mathbb{T}^k)$

After this discourse into general trait-dependent ODE community-dynamical systems we continue the discussion of Lotka-Volterra community-dynamical systems. We mention several properties that will play a role in the context of adaptive dynamics.

In  $\mathbb{T}^k$ , the sets  $V_{k,\sigma}$ ,  $\sigma \in \Sigma_k$ , are clearly exchangeable under permutation, and are separated from each other by the diagonal hyperplanes  $\Delta_{i,j}^k$ ,  $1 \leq i < j \leq k$ . Furthermore, they are pairwise disjoint, and  $\bigcup_{\sigma \in \Sigma_k} V_{k,\sigma} = \mathbb{T}^k \setminus \Delta^k$ . Consequently, the collection of Lotka-Volterra community dynamics covered by  $LV_k(\mathbb{T}^k)$  is fully described by the subclass of Lotka-Volterra models  $\bigcup_{i=1}^k LV_k(V_{i,\sigma_0})$ .

The determinant of the interaction matrix at  $(\tau_1, \dots, \tau_k)$ ,  $|A(\tau_1, \dots, \tau_k)|$ , is invariant under a permutation of the coordinates, i.e., invariant under composition of reflections of  $(\tau_1, \dots, \tau_k)$  over any of the diagonal hyperplanes  $\Delta_{i,j}^k$ . Its value on each of the diagonal hyperplanes is equal to 0. We introduce the following notation pertaining to determinants.

**Notation 2.** For  $V \subset \mathbb{T}^k$ , we write  $D(V)$  for the set of elements in  $V$  for which the interaction determinant equals 0:

$D(V) = \{(\tau_1, \dots, \tau_k) \in V \mid |A(\tau_1, \dots, \tau_k)| = 0\}$ ; its complement in  $V$  shall be denoted by  $R(V)$ :  $R(V) = \{(\tau_1, \dots, \tau_k) \in V \mid |A(\tau_1, \dots, \tau_k)| \neq 0\}$ .

An element of  $D(V)$ , as well as the community dynamics it represents, will be called *degenerate*; an element of  $R(V)$  as well as its corresponding dynamics will be called *regular*. (Another possible name for an element of  $D(V)$  could be *singular*; this term, however, will be used to characterise adaptive-dynamical properties of trait combinations.)

We introduce the following notation for extinction boundaries for  $LV_k(\tau_1, \dots, \tau_k)$ .

**Notation 3.** For  $i_1, \dots, i_l \in \{1, \dots, k\}$ ,  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$  denotes the set  $\{(x_1, \dots, x_k) \in \mathbb{R}_+^k \mid x_{i_1} = \dots = x_{i_l} = 0\}$ . It is a subset of  $\text{bd}(\mathbb{R}_+^k) = \{(x_1, \dots, x_k) \in \mathbb{R}_+^k \mid \exists i \in \{1, \dots, k\} : x_i = 0\}$ , the boundary set of  $\mathbb{R}_+^k$ .

By the property of reduction by absence introduced above, on  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$  the Lotka-Volterra model  $LV_k(\tau_1, \dots, \tau_k)$  reduces to  $LV_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$ .

If  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  is such that  $LV_k(\tau_1, \dots, \tau_k)$  allows for a rest point in the interior of the community state space, then this rest point is unique.

**Notation 4.**

1. For a subset  $V \subset \mathbb{T}^k$  or  $V \subset \mathbb{R}_+^k$ ,  $\text{int}(V)$  denotes the interior of  $V$ .

Let  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$ .

2. A general rest point of  $LV_k(\tau_1, \dots, \tau_k)$  in the community state space  $\mathbb{R}_+^k$  will be denoted by  $x^* = (x_1^*, \dots, x_k^*)$  (or, if convenient, by  $(x_1^*, \dots, x_k^*)(\tau_1, \dots, \tau_k)$  or  $(x_1^*(\tau_1, \dots, \tau_k), \dots, x_k^*(\tau_1, \dots, \tau_k))$ ).
3. A rest point of  $LV_k(\tau_1, \dots, \tau_k)$  in the interior of  $\mathbb{R}_+^k$  that is unique will be denoted by  $\hat{x} = (\hat{x}_1, \dots, \hat{x}_k)$ , and with the same notational conventions as in 2). Such a rest point necessarily satisfies the set of equations

$$r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j)x_j = 0, \quad i = 1, \dots, k. \tag{5.4}$$

For  $V \subset \mathbb{T}^k$ , we denote with  $R_{\text{int}}(V)$  the subset of trait combinations  $(\tau_1, \dots, \tau_k) \in R(V)$  for which the unique  $\hat{x} \in \text{int}(\mathbb{R}_+^k)$  exists.

If in a  $LV_k(\tau_1, \dots, \tau_k)$  two trait values  $\tau_i$  and  $\tau_j$  are such that both  $a(\tau_i, \tau_j) < 0$  and  $a(\tau_j, \tau_i) < 0$ , then the populations  $i$  and  $j$  are said to be in a competitive relationship. Interaction between two populations that are in a competitive relationship causes a negative contribution to their per capita growth rates. If all interaction coefficients  $a(\tau_i, \tau_j)$  are strictly negative, then  $LV_k(\tau_1, \dots, \tau_k)$  is called a fully competitive Lotka-Volterra model. In a fully competitive Lotka-Volterra model the per capita growth rates of all populations decrease due to the interactions within and between the populations. Clearly a fully competitive Lotka-Volterra model has uniformly bounded orbits. Opposite to a competitive relationship is a cooperative (or mutualistic) relationship: two populations  $i$  and  $j$  in  $LV_k(\tau_1, \dots, \tau_k)$  are in a cooperative relationship if the respective traits  $\tau_i$  and  $\tau_j$  satisfy  $a(\tau_i, \tau_j) > 0$  and  $a(\tau_j, \tau_i) > 0$ . Interactions between two populations that are in a cooperative relationship cause positive contributions to the per capita growth rates of these populations. (For an extensive study on competitive and cooperative systems see [46], [47], [48].) In the asymmetric case in which two traits  $\tau_i$  and  $\tau_j$  satisfy  $a(\tau_i, \tau_j) > 0$  and  $a(\tau_j, \tau_i) < 0$  exploitation takes place, in which population  $i$  is the exploiter and exploits population  $j$  (and population  $j$  is being exploited by population  $i$ ). Exploitation occurs in host-parasite (or prey-predator) relationships. Finally, if two traits  $\tau_i$  and  $\tau_j$  satisfy  $a(\tau_i, \tau_j) = 0$ , then population  $j$  is said to be neutral with respect to population  $i$ . An extensive study on competitive and cooperative systems is

Theorem 15.2.1 in [49] on uniform boundedness implies the following

**Lemma 1.**

1. The orbits of equation (5.1) for a single population with trait value  $\tau$  and density  $x$  ( $= x_\tau$ ) are uniformly bounded for  $t \rightarrow +\infty$  if and only if the interaction function  $a$  satisfies:  $a(\tau, \tau) < 0$ .
2. The orbits of the Lotka-Volterra equations (5.1) for two populations with trait values  $\tau_1$  and  $\tau_2$  are uniformly bounded for  $t \rightarrow +\infty$  if and only if  $a(\tau_1, \tau_1) < 0$  and  $a(\tau_2, \tau_2) < 0$  and, in case of a cooperative interaction between the two populations,  $|A(\tau_1, \tau_2)| = a(\tau_1, \tau_1)a(\tau_2, \tau_2) - a(\tau_1, \tau_2)a(\tau_2, \tau_1) > 0$ .

The previous Lemma implies that  $a(\tau_i, \tau_i) < 0$ ,  $i = 1, \dots, k$ , is a necessary condition on the contypic interaction coefficients for the solutions of the equations (5.1) to be



uniformly bounded (for any function  $r$ ). We therefore shall assume this condition to hold from now on:

**Assumption 2.** For all  $\tau \in \mathbb{T}$ :  $a(\tau, \tau) < 0$ .

Continuity of the function  $a$  implies:

**Corollary 1.** Let  $k \geq 2$ , and  $i, j \in \{1, \dots, k\}$  with  $i \neq j$ . For each  $\tau \in \mathbb{T}$  there exists a non-empty neighbourhood  $U_\tau$  of  $\tau$  in  $\mathbb{T}$  such that for any choice of  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  with  $\tau_i, \tau_j \in U_\tau$ , the corresponding populations  $i$  and  $j$  in  $LV_k(\tau_1, \dots, \tau_k)$  are in a competitive relationship.

**Remark 2.** By means of the density transformation  $x \mapsto a(\tau, \tau)x$  we may rewrite the equations (5.1) to obtain a Lotka-Volterra model for the  $k$  populations with the contypic interaction coefficients  $a(\tau_i, \tau_i)$  for all  $i \in \{1, \dots, k\}$  equal to  $-1$ . We shall however not explicitly assume this here.

For later use we also recall the definition of permanence (see also [49], chapter 13 Section 1):

**Definition 2.**  $LV_k(\tau_1, \dots, \tau_k)$  is called permanent if there exist  $\delta > 0$  and  $D > 0$  such that whenever  $x_i > 0$  for all  $i = 1, \dots, k$ , then

1.  $\delta < \liminf_{t \rightarrow +\infty} x_i(t)$  for all  $i$  (with  $\delta$  independent of the  $x_i(0)$ ),

and in addition

2.  $\limsup_{t \rightarrow +\infty} x_i(t) \leq D$  for all  $i$ .

If a community-dynamical system is permanent, sufficiently small perturbations in any of the densities cannot lead to extinction of one or more of the populations.

After this discussion of Lotka-Volterra community-dynamical systems we turn our attention to attractors, and make the first steps towards adaptive dynamics.

#### 5.2.4 $c$ -Attractors and invasion fitness: from community dynamics towards adaptive dynamics

In this paper we are i.a. interested in the fate of resident and mutant populations after emergence of the mutants from the community of residents. Due to the

initially very low density of a mutant population, invasion of the environment it encounters, by increase of its density, is subject to demographic stochasticity. Whether or not a mutant population has a positive probability to invade an environment depends, amongst others, on the phenotypic trait of the mutants, and is captured by the invasion fitness of the mutants' phenotypic trait value in that environment.

**Definition 3.** The invasion fitness of the phenotypic trait value of a mutant population with respect to an environment is the long-term averaged initial per capita growth rate (or transversal Lyapunov exponent) of the mutant population in that environment.

The general idea of this definition of invasion fitness is discussed in [73] and [72]. Throughout the paper we shall vary our terminology when talking about the invasion fitness of a phenotypic trait value: also the invasion fitness of a phenotypic trait, the invasion fitness of a phenotype, the invasion fitness of a trait, or simply the invasion fitness or fitness, are being used, and all these come down to the same notion.

A mutant population in an environment whose phenotype has a positive invasion fitness, has a positive probability to invade that environment, and is called *successful*. A mutant population in an environment for which the phenotype has a non-positive invasion fitness has a zero probability to invade that environment, and is called *unsuccessful*; it disappears after a relatively short time (on the community-dynamical timescale) and leaves the phenotypic composition of the environment unaltered. (For details on the relation between positive invasion fitness and the non-zero probability of invasion see e.g. [11] and [61].) Concerning the occurrence of mutants we make the following assumption.

**Assumption 3.** There is a separation between the timescale on which a community-dynamical attractor is approached and that on which successful mutant populations occur.

Assumption 3 forms the basis for the working hypothesis that only a single successful mutant population may emerge, from a community that resides on an attractor. In the case of successful mutants we shall concentrate on those invasion attempts where the mutants make it to such densities that the deterministic

description in terms of ODE's is applicable. We shall soon provide more details about the notion of attractor that we adopt in the paper.

In general, for the invasion fitness of a mutant population's phenotype to be well-defined it is required that the environment that the mutants encounter is ergodic. In case a mutant population interacts with a resident community according to a Lotka-Volterra community dynamics, the constraint on ergodicity can however be relaxed (see Corollary 4.1). The invasion fitness of the phenotype of the mutant population in the environment set by the resident attractor then can be calculated whenever the densities of the resident populations evolve in time along an orbit that is confined to a closed and bounded set in the interior of the residents' community state space. So-called extinction-preserving chain attractors qualify as such sets. The notion of chain attractor is an appropriate attractor notion for dynamical systems subject to arbitrarily small perturbations. In such a system, while converging to an  $\omega$ -limit set, arbitrarily small perturbations may transfer the dynamics from its stable manifold to its unstable manifold (if the latter exists). A chain attractor is the resulting configuration the dynamics eventually will reside on. The notion of extinction preserving chain attractor (ep-chain attractor) is that of chain attractor, but adapted to dissipative immigration-free community processes, in which populations can go extinct at low densities and then cannot be rescued by noise (see [52]). An ep-chain attractor therefore necessarily lies either in the interior of the community state space, or in the interior of one of its extinction boundaries. In [52] it is derived that in general an ep-chain attractor is a closed and bounded set. (Note that the dynamics restricted to an ep-chain attractor necessarily is permanent.) By definition, for any  $k \geq 1$  the point  $(0, \dots, 0) \in \mathbb{R}_+^k$  is an ep-chain attractor. We shall show that in the context of Lotka-Volterra community dynamics, the invasion fitness of a mutant phenotype is independent of the specific ep-chain attractor in the interior of a community state space on which the mutants emerge, and that we therefore are allowed to speak simply of the invasion fitness of that phenotype with respect to the resident trait values. (We shall however not include noise in the dynamics, nor in the mathematical concepts derived from it: we assume a deterministic Lotka-Volterra community dynamics, but adopt the attractor notion

for such dynamics under arbitrarily small perturbations.) We continue with the following

**Assumption 4.**

1. We assume that when a mutant population emerges, the resident community moves along an orbit in an ep-chain attractor, which is a closed and bounded subset in the interior of the resident community dynamics state space. We shall denote such an attractor as  $c$ -attractor, where the  $c$  stems from community.
2. Throughout the paper we assume that on a  $c$ -attractor only one mutant population emerges at a time, in a very small positive density, from one of the populations present on that attractor.  $M(\tau)$  denotes the set of possible phenotypic trait values of mutant populations that can emerge from the resident population with trait value  $\tau$ , and is called the mutational range of  $\tau$ . We suppose that there exist two positive numbers  $\epsilon_-(\tau)$  and  $\epsilon_+(\tau)$  such that  $M(\tau)$  can be written as  $M(\tau) = \{v \in \mathbb{T} \mid \tau - \epsilon_-(\tau) < v < \tau + \epsilon_+(\tau)\}$ . (Note that this allows for the degenerate case in which the mutants' phenotypic trait value is equal to that of its progenitors. Mutants and progenitors then are indistinguishable, and the system of only residents is phenotypically equivalent to that of residents and mutants.) Two sets  $M(\tau_i)$  and  $M(\tau_j)$  are not necessarily disjoint. With  $x_\nu$  we denote the mutant population's density for mutants with phenotypic trait value  $\nu$ .
3. After the emergence of a mutant population with trait value  $\nu \in \mathbb{T}$  from a  $c$ -attractor for  $LV_k(\tau_1, \dots, \tau_k)$ , the densities of residents and mutants develop in time according to the community-differential equations (5.1) for  $LV_{k+1}(\tau_1, \dots, \tau_k, \nu)$ .

We now determine the invasion fitness of a mutants' phenotypic trait value in the context of Lotka-Volterra community dynamics, and discuss its implications. We start with the following general property of mappings  $t \mapsto x(t)$ ,  $t \geq 0$  for which the image is restricted to a closed and bounded subset in the interior of  $\mathbb{R}_+^k$ ,

$k \geq 1$ . (Note that we do not require the mapping  $t \mapsto x(t)$  to be continuous; in particular, it is not required here that  $x(t), t \geq 0$  is a solution of (5.1)).

**Lemma 2.** Let  $\mathbb{R}_+ \rightarrow U \subset \text{int}(\mathbb{R}_+^k)$ ,  $t \mapsto x(t) = (x_1(t), \dots, x_k(t))$ , denote a mapping into a closed and bounded subset  $U$  in the interior of  $\mathbb{R}_+^k$ ,  $k \geq 1$ . Then for each  $i = 1, \dots, k$ :  $\lim_{t \rightarrow +\infty} \frac{\log(x_i(t))}{t} = 0$ .

**Proof** The proof of this statement is straightforward:  $\limsup_{t \rightarrow +\infty} \frac{\log(x_i(t))}{t} = 0$  follows from the assumption on boundedness of  $x(t)$  (in principle uniform boundedness of  $x(t)$  for  $t \rightarrow +\infty$  would suffice here);  $\liminf_{t \rightarrow +\infty} \frac{\log(x_i(t))}{t} < 0$  would contradict that  $\{x(t) | t \geq 0\}$  lies in a closed subset in the interior of  $\mathbb{R}_+^k$ .

Suppose the mutant population emerges from population  $i$  on an orbit of (5.1) in a  $c$ -attractor in the interior of  $\mathbb{R}_+^k$ . The possible invasion fitnesses for the mutants' phenotypic trait values  $v \in M(\tau_i)$  are considered to be a function in  $v$  in which the resident trait values  $\tau_1, \dots, \tau_k$  appear as parameters. This function is called the *invasion fitness function* on the specific orbit on which the mutants appear. Formally invasion fitness is a valid notion for any trait value  $v \in \mathbb{T}$ , and extends beyond the biologically restricted set  $\bigcup_{i=1}^k M(\tau_i)$  of possible mutant trait values that may emerge from a community of resident populations carrying traits  $\tau_1, \dots, \tau_k$ . Therefore the domain of the invasion fitness function is taken to be  $\mathbb{T}$  rather than  $\bigcup_{i=1}^k M(\tau_i)$ , and its argument may refer to the phenotypic trait value of any population that tries to invade the resident community in an initially very small positive density.

**Notation 5.**  $s_k(\tau_1, \dots, \tau_k; \cdot) : \mathbb{T} \rightarrow \mathbb{R}$  denotes the invasion fitness function on an orbit in a  $c$ -attractor in the interior of  $\mathbb{R}_+^k$ .

The parameters  $\tau_1, \dots, \tau_k$  appear in the argument of the invasion fitness function, and are separated from the mutants' trait value by means of a semicolon. By doing so we can make a clear distinction between the resident trait values and possible operations performed on them (such as a permutation, or a reduction due to absence of a resident population), and the mutants' trait value. Furthermore, by letting the parametric resident traits appear in the argument of the invasion fitness function rather than as an index to it, we adapt already here to a notation that

will only become effective in the second part of the text, where we will consider functional dependence of the mutants' fitness on the resident trait values. By adopting this notation we already anticipate on the result that the invasion fitness of a phenotype is independent of the specific  $c$ -attractor in  $\text{int}(\mathbb{R}_+^k)$ , or specific orbit herein, on which the mutants appear; see Corollary 3. Therefore it suffices to refer to the resident community solely by means of the phenotypic trait values present in it.

From the definition of invasion fitness and equations (5.1) we derive that:

$$s_k(\tau_1, \dots, \tau_k; \nu) = \lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \left( \frac{1}{x_\nu(t)} \frac{d}{dt} x_\nu(t) \right) \Big|_{x_\nu(t)=0} =$$

$$\lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \left( r(\nu) + \sum_{i=1}^k a(\nu, \tau_i) x_i(t) \right) dt = r(\nu) + \sum_{i=1}^k a(\nu, \tau_i) \bar{x}_i. \quad (5.5)$$

Here  $\bar{x}_i = \bar{x}_i(\tau_1, \dots, \tau_k) = \lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T x_i(t) dt$  exists, and denotes the time average of the density of population  $i$  along the specific orbit followed by the resident community. This average density  $\bar{x}_i$  in general depends on trait value  $\tau_i$  as well as on the trait values of the other resident populations. The fact that this average density exists follows from the confinement of the density  $x_i$  at any time to a closed and bounded set in the interior of  $\mathbb{R}_+$ ; see also e.g. the first part of the proof of Theorem 5.2.3 in [49]. (At this point it is not yet allowed to conclude that this average is independent of the specific orbit followed; this can only be done with additional results that we derive below in Lemma 3.)

The densities of the populations present on an orbit in  $\text{int}(\mathbb{R}_+^k)$  do not become zero nor increase to infinity. Therefore it intuitively is clear that the trait value of a resident population has a zero invasion fitness with respect to the environment that this population itself belongs to.

**Lemma 3.** For  $i = 1, \dots, k$ :  $s_k(\tau_1, \dots, \tau_k; \tau_i) = 0$ .

The proof of this statement goes as follows. Consider  $k + 1$  populations, with trait values  $\tau_1, \dots, \tau_k, \tau_{k+1}$ , respectively, of which the  $k + 1$ -th population is the mutant

population, with trait value  $\tau_{k+1} = \tau_i$  for some  $i \in \{1, \dots, k\}$ , that appears on a c-attractor component for  $LV_k(\tau_1, \dots, \tau_k)$ . Then

$$s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) = \lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \left( \frac{1}{x_{k+1}(t)} \frac{d}{dt} x_{k+1}(t) dt \right) \Big|_{x_{k+1}(t)=0} =$$

$$\lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \left( r(\tau_{k+1}) + \sum_{j=1}^k a(\tau_{k+1}, \tau_j) x_j(t) \right) dt. \quad (5.6)$$

Since  $\tau_{k+1} = \tau_i$ , this last expression is equal to

$$\lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \left( r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j) x_j(t) \right) dt = \lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \frac{1}{x_i(t)} \frac{d}{dt} x_i(t) dt =$$

$$\lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T \frac{1}{x_i(t)} dx_i(t) = \lim_{T \rightarrow +\infty} \frac{1}{T} \int_0^T d \log(x_i(t)) =$$

$$\lim_{T \rightarrow +\infty} \frac{\log(x_i(T)) - \log(x_i(0))}{T} = 0 \quad (5.7)$$

(by Lemma 2), which proves the statement.

The  $k$  equalities  $s_k(\tau_1, \dots, \tau_k; \tau_i) = 0$ ,  $i = 1, \dots, k$  yield  $k$  expressions

$$r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j) \bar{x}_j = 0, \quad i = 1, \dots, k, \quad (5.8)$$

that imply the following

**Corollary 2.** Let  $(x^t)_{t \geq 0}$  denote an orbit of  $LV_k(\tau_1, \dots, \tau_k)$  in a closed and bounded subset in the interior of  $\mathbb{R}_+^k$ . Then for each  $i = 1, \dots, k$  the average density  $\bar{x}_i(\tau_1, \dots, \tau_k)$  is uniquely determined (and necessarily equal to the positive equilibrium density  $\hat{x}_i(\tau_1, \dots, \tau_k)$ ) if and only if  $(\tau_1, \dots, \tau_k) \in R_{int}(\mathbb{T}^k)$ .

Thus, if  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ , the existence of an orbit  $(x^t)_{t \geq 0}$  confined to a closed and bounded set in the interior of  $\mathbb{R}_+^k$  implies the existence of a unique interior rest point for  $LV_k(\tau_1, \dots, \tau_k)$ , i.e., then  $(\tau_1, \dots, \tau_k) \in R_{int}(\mathbb{T}^k)$ .

**Remark 3.** Corollary 2 is put slightly stronger than Theorem 5.2.3 in [49]. This Theorem assumes that the densities  $x_1, \dots, x_k$  of  $k$  populations develop according to a Lotka-Volterra community dynamics for which there exist a unique equilibrium

density  $\hat{x} = (\hat{x}_1, \dots, \hat{x}_k) \in \text{int}(\mathbb{R}_+^k)$ . Then, if there exist two positive numbers  $a$  and  $A$  such that  $a < x_i(t) < A$  for all  $i$  and all  $t > 0$ , the average density  $\bar{x}_i$  exists and equals  $\hat{x}_i$ .

**Corollary 3.** If  $(\tau_1, \dots, \tau_k) \in R_{\text{int}}(\mathbb{T}^k)$ , then the function  $s_k(\tau_1, \dots, \tau_k; \cdot)$  is well-defined, in the sense that  $s_k(\tau_1, \dots, \tau_k; \nu)$  is independent of the specific orbit the resident community follows, in any of the possible  $c$ -attractors for  $LV_k(\tau_1, \dots, \tau_k)$ .

The previous Corollary allows us to define the invasion fitness of the mutants' phenotype on a  $c$ -attractor.

**Notation 6.**

1. For each  $k \geq 1$ , an element  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  for which there exists a  $c$ -attractor for  $LV_k(\tau_1, \dots, \tau_k)$  in  $\text{int}(\mathbb{R}_+^k)$  will be denoted by  $\langle \tau_1, \dots, \tau_k \rangle$ .
2. For a given  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  the set  $\text{Att}(\tau_1, \dots, \tau_k)$  denotes the collection of  $c$ -attractors for  $LV_k(\tau_1, \dots, \tau_k)$  in  $\text{int}(\mathbb{R}_+^k)$ . However, for specific choices of  $(\tau_1, \dots, \tau_k)$  this set can be empty.
3. The collection of elements  $\langle \tau_1, \dots, \tau_k \rangle$ , for all  $(\tau_1, \dots, \tau_k) \in R_{\text{int}}(\mathbb{T}^k)$ , is denoted by  $\mathbb{A}_k$ .

An element of  $\mathbb{A}_1$  is referred to as a *monomorphism*. For  $k \geq 2$ , an element of  $\mathbb{A}_k$  in general is called *polymorphism* or *k-morphism*, with the additional nomenclature *dimorphism* for an element of  $\mathbb{A}_2$ , and *trimorphism* for an element that belongs to  $\mathbb{A}_3$ . We shall take this nomenclature also to hold for a  $c$ -attractor in the respective  $\text{int}(\mathbb{R}_+^k)$ .

It follows straightforwardly that  $\mathbb{A}_k \subset R_{\text{int}}(\mathbb{T}^k)$ . Based on expression (5.5) and Corollaries 2 and 3 we obtain:

**Corollary 4.** Let  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$ .

- 1.

$$s_k(\tau_1, \dots, \tau_k; \nu) = r(\nu) + \sum_{i=1}^k a(\nu, \tau_i) \hat{x}_i(\tau_1, \dots, \tau_k). \tag{5.9}$$

Therefore, in case of multiple  $c$ -attractors represented by  $\langle \tau_1, \dots, \tau_k \rangle$ , mutants do not discriminate between these attractors with regard to invasion. These  $c$ -attractors then are said to be *evolutionary equivalent with regard to invasion*.



2. The function  $s_k(\tau_1, \dots, \tau_k; \cdot) : \mathbb{T} \rightarrow \mathbb{R}$  inherits the differentiability properties from the functions  $r$  and  $a$ .
3. For each  $\sigma \in \Sigma_k$ , and for all  $\nu \in \mathbb{T}$ :  $s_k(\tau_1, \dots, \tau_k; \nu) = s_k(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}; \nu)$ .

The origin  $0 \in \mathbb{R}_+^0$  is a  $c$ -attractor by definition, on which no traits are present; it shall be denoted by  $\lambda$  (see Notation 1.3.). We make the following definition with respect to  $\lambda$ , to be used in the next section.

**Definition 4.**

1.  $\hat{x}(\lambda) = 0$ .
2.  $|A(\lambda)| = 1$ .
3. The invasion fitness function on  $\lambda$  is  $s_0(\lambda; \cdot) : \mathbb{T} \rightarrow \mathbb{R}$ ,  $s_0(\lambda; \nu) = r(\nu)$ ; it will simply be denoted by  $s_0$  (omitting the  $\lambda$ ).

**Remark 4.**

1. The third statement in Corollary 4 states that the ordering of the traits present on a resident  $c$ -attractor does not influence the fitness of the mutants' trait. In particular this implies that the order in evolutionary time in which the resident populations were subsequently incorporated to form a  $c$ -attractor, does not affect the fitness of mutants that emerge from that attractor.
2. Note that the notational conventions introduced so far for elements  $(\tau_1, \dots, \tau_k)$  of  $\mathbb{T}^k$  do not automatically extend to the bracket notation  $\langle \tau_1, \dots, \tau_k \rangle \in R_{int}(\mathbb{T}^k)$ . E.g., the notation  $\langle \tau_1, \dots, \tau_k \setminus \tau_k \rangle$  and its identification with  $\langle \tau_1, \dots, \tau_{k-1} \rangle$  only make sense if there exists a  $c$ -attractor in the interior of the community state space of  $LV_{k-1}(\tau_1, \dots, \tau_{k-1})$ . However, for each  $\sigma \in \Sigma_k$ ,  $\langle \tau_1, \dots, \tau_k \rangle$  can be identified with  $\langle \tau_{\sigma(1)}, \dots, \tau_{\sigma(k)} \rangle$ .
3. Two Lotka-Volterra models  $LV_k(\tau_1, \dots, \tau_k)$  and  $LV_l(\tau'_1, \dots, \tau'_l)$  that are phenotypically equivalent do not necessarily have equal collections of  $c$ -attractors. As a consequence the equality of functions  $s_k(\tau_1, \dots, \tau_k; \cdot) = s_l(\tau'_1, \dots, \tau'_l; \cdot)$  may not hold true. In fact, let  $k > l$ , and suppose that  $LV_k(\tau_1, \dots, \tau_k)$  is phenotypically equivalent to  $LV_l(\tau'_1, \dots, \tau'_l)$ ,

with the latter admitting a global  $c$ -attractor. Then  $LV_k(\tau_1, \dots, \tau_k)$  will have no  $c$ -attractors, and any dynamics that starts in the interior of  $\mathbb{R}_+^k$  eventually will converge to the global  $c$ -attractor for  $LV_l(\tau'_1, \dots, \tau'_l)$ . For example, suppose that  $LV_1(\tau)$  has a unique  $c$ -attractor  $\langle \tau \rangle$ .  $LV_2(\tau, \tau)$  has no  $c$ -attractor; it has a line of neutral equilibria which connects the two boundary equilibria in the two state spaces for the two populations separately. These two boundary equilibria are  $c$ -attractors for the two respective single dynamics as well as for the combined dynamics. The line of equilibria in the interior of the combined dynamics is however not a  $c$ -attractor: arbitrarily small perturbations eventually will drive a community present on this line to either one of the two boundary attractors. The function  $s_1(\tau; \cdot)$  is well-defined; the function  $s_2(\tau, \tau; \cdot)$  however is not well-defined, because the determinant of the interaction matrix equals 0. In a later section we shall construct well-defined extensions of functions  $s_k(\tau_1, \dots, \tau_k; \cdot)$  to cases for which  $(\tau_1, \dots, \tau_k) \in \Delta^k$ .

4. By Definition 4 we may write  $R(\mathbb{T}^0) = \mathbb{A}_0 = \{\lambda\}$ .

**Example 1.**

1. For  $k = 1$  equations (5.1) reduce to

$$\frac{d}{dt}x = x(r(\tau) + a(\tau, \tau)x), \tag{5.10}$$

and it follows immediately that each  $\tau \in \mathbb{T}$  with  $r(\tau) > 0$  corresponds unequivocally with a unique point-attractor  $\langle \tau \rangle$  in the interior of the population state space, with  $\hat{x}_\tau = \hat{x}_\tau \langle \tau \rangle = -\frac{r(\tau)}{a(\tau, \tau)}$ . Thus,  $\mathbb{A}_1 = \{\tau \in \mathbb{T} | r(\tau) > 0\}$ . If  $r(\tau) \leq 0$ , then the origin 0 is the unique  $c$ -attractor for  $LV_1(\tau)$  and  $Att(\tau) = \emptyset$ . From expression (5.9) it follows that for  $\tau \in \mathbb{A}_1$ :

$$s_1(\tau; \nu) = r(\nu) - r(\tau) \frac{a(\nu, \tau)}{a(\tau, \tau)}. \tag{5.11}$$

2. For  $k = 2$ , the community-dynamical differential equations become

$$\begin{cases} \frac{d}{dt}x_1 = x_1(r(\tau_1) + a(\tau_1, \tau_1)x_1 + a(\tau_1, \tau_2)x_2) \\ \frac{d}{dt}x_2 = x_2(r(\tau_2) + a(\tau_2, \tau_1)x_1 + a(\tau_2, \tau_2)x_2) \end{cases} \tag{5.12}$$

Straightforward analysis tells that there exists a unique  $c$ -attractor  $\langle \tau_1, \tau_2 \rangle$  in the interior of the community state space if and only if  $\tau_1$  and  $\tau_2$  satisfy the following three constraints:

$$\begin{cases} r(\tau_1)a(\tau_2, \tau_1) > r(\tau_2)a(\tau_1, \tau_1), \\ r(\tau_2)a(\tau_1, \tau_2) > r(\tau_1)a(\tau_2, \tau_2), \\ |A(\tau_1, \tau_2)| > 0, \text{ i.e., } a(\tau_1, \tau_1)a(\tau_2, \tau_2) > a(\tau_1, \tau_2)a(\tau_2, \tau_1). \end{cases}$$

This  $c$ -attractor is a point-attractor, its basin of attraction is  $\text{int}(\mathbb{R}_+^2)$ . Thus,

$$\mathbb{A}_2 = \{(\tau_1, \tau_2) \in \mathbb{T}^2 \mid r(\tau_1)a(\tau_2, \tau_1) > r(\tau_2)a(\tau_1, \tau_1), \\ r(\tau_2)a(\tau_1, \tau_2) > r(\tau_1)a(\tau_2, \tau_2), |A(\tau_1, \tau_2)| > 0\}. \quad (5.13)$$

At  $\langle \tau_1, \tau_2 \rangle$  the equilibrium densities are

$$\begin{aligned} (\hat{x}_1\langle \tau_1, \tau_2 \rangle, \hat{x}_2\langle \tau_1, \tau_2 \rangle) = \\ \left( \frac{-r(\tau_1)a(\tau_2, \tau_2) + r(\tau_2)a(\tau_1, \tau_2)}{a(\tau_1, \tau_1)a(\tau_2, \tau_2) - a(\tau_1, \tau_2)a(\tau_2, \tau_1)}, \frac{r(\tau_1)a(\tau_2, \tau_1) - r(\tau_2)a(\tau_1, \tau_1)}{a(\tau_1, \tau_1)a(\tau_2, \tau_2) - a(\tau_1, \tau_2)a(\tau_2, \tau_1)} \right). \end{aligned} \quad (5.14)$$

Figure 5.1 shows for  $\mathbb{T} = [-1, 1]$  the non-empty set  $\mathbb{A}_2$  in  $(-1, 1)^2$ , for  $r(\tau) = 1 - \tau^2$ , and  $a(\tau_1, \tau_2) = -\frac{e^{-3(\tau_1 - \tau_2)^2}}{1 - 0.5\tau_1^2}$ . The set  $\mathbb{A}_1$  in this case is equal to  $(-1, 1)$  and is embedded in the main diagonal in  $\mathbb{T}^2$ . Note that  $\mathbb{A}_2$  is symmetric under reflection over the diagonal  $\tau_1 = \tau_2$  of  $\mathbb{T}^2$ , in agreement with the phenotypic equivalence under permutations of  $LV_2(\tau_1, \tau_2)$  and  $LV_2(\tau_2, \tau_1)$ .

For  $\langle \tau_1, \tau_2 \rangle \in \mathbb{A}_2$  we find that

$$s_2(\tau_1, \tau_2; \nu) = r(\nu) + a(\nu, \tau_1)\hat{x}_1\langle \tau_1, \tau_2 \rangle + a(\nu, \tau_2)\hat{x}_2\langle \tau_1, \tau_2 \rangle, \quad (5.15)$$

with  $\hat{x}_1\langle \tau_1, \tau_2 \rangle$  and  $\hat{x}_2\langle \tau_1, \tau_2 \rangle$  as in expression (5.14). Note that for each  $\nu$  the equality  $s_2(\tau_1, \tau_2; \nu) = s_2(\tau_2, \tau_1; \nu)$  holds, and that the equilibrium densities follow from the two equations  $s_2(\tau_1, \tau_2; \tau_1) = 0$  and  $s_2(\tau_1, \tau_2; \tau_2) = 0$ . A little algebra shows that for  $(\tau_1, \tau_2) \in \mathbb{A}_2 \cap (\mathbb{A}_1 \times \mathbb{A}_1)$  expression (5.14) equals

$$(\hat{x}_1\langle \tau_1, \tau_2 \rangle, \hat{x}_2\langle \tau_1, \tau_2 \rangle) = -\frac{1}{|A(\tau_1, \tau_2)|} (a(\tau_2, \tau_2)s_1(\tau_2; \tau_1), a(\tau_1, \tau_1)s_1(\tau_1; \tau_2)), \quad (5.16)$$

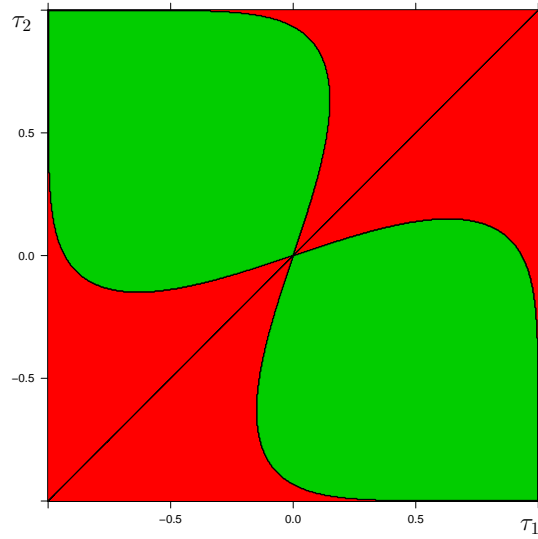


Figure 5.1: For  $\mathbb{T} = [-1, 1]$  and functions  $r(\tau) = 1 - \tau^2$ ,  $a(\tau_1, \tau_2) = -\frac{e^{-3(\tau_1 - \tau_2)^2}}{1 - 0.5\tau_1^2}$ , the main diagonal in  $\mathbb{T}^2$  contains the embedded set of monomorphisms  $\mathbb{A}_1 = (-1, 1)$ . The green region (in  $(-1, 1)^2$ ) shows the set  $\mathbb{A}_2$  of dimorphisms. In this region both  $s_1(\tau_1; \tau_2)$  and  $s_1(\tau_2; \tau_1)$  are positive. On the main diagonal and on the black curves either  $s_1(\tau_1; \tau_2)$  or  $s_1(\tau_2; \tau_1)$  equals 0. In the red region at least one of  $s_1(\tau_1; \tau_2)$  and  $s_1(\tau_2; \tau_1)$  is negative.

and that expression (5.15) is equal to

$$s_2(\tau_1, \tau_2; \nu) = \frac{r(\tau_1)s_1(\tau_1; \tau_2)s_1(\tau_2; \nu) + r(\tau_2)s_1(\tau_2; \tau_1)s_1(\tau_1; \nu) - r(\nu)s_1(\tau_1; \tau_2)s_1(\tau_2; \tau_1)}{r(\tau_1)s_1(\tau_1; \tau_2) + r(\tau_2)s_1(\tau_2; \tau_1) - s_1(\tau_1; \tau_2)s_1(\tau_2; \tau_1)}. \quad (5.17)$$

The last expression can be rewritten as

$$s_2(\tau_1, \tau_2; \nu) = \frac{\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & s_1(\tau_1; \nu) \\ s_1(\tau_2; \tau_1) & 0 & s_1(\tau_2; \nu) \\ r(\tau_1) & r(\tau_2) & r(\nu) \end{pmatrix} \right|}{\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & 1 \\ s_1(\tau_2; \tau_1) & 0 & 1 \\ r(\tau_1) & r(\tau_2) & 1 \end{pmatrix} \right|}. \quad (5.18)$$

**Remark 5.**

1. From Examples 1.1 and 1.2 and expression (5.11) it follows that the set of dimorphisms  $\mathbb{A}_2 \cap (\mathbb{A}_1 \times \mathbb{A}_1)$  can be characterised as:

$$\mathbb{A}_2 \cap (\mathbb{A}_1 \times \mathbb{A}_1) = \{(\tau_1, \tau_2) \in \mathbb{T}^2 | r(\tau_1) > 0, r(\tau_2) > 0, \\ s_1(\tau_1; \tau_2) > 0, s_1(\tau_2; \tau_1) > 0, |A(\tau_1, \tau_2)| > 0\}. \quad (5.19)$$

Thus,  $\mathbb{A}_2 \cap (\mathbb{A}_1 \times \mathbb{A}_1)$  can be constructed by taking the intersection of the set of points  $(\tau_1, \tau_2)$  in  $\mathbb{A}_1 \times \mathbb{A}_1$  for which  $s_1(\tau_1; \tau_2) > 0$  with its reflection over the diagonal  $\tau_1 = \tau_2$  and with the set of points on which the interaction matrix has a positive determinant. Intersections of regions of positive fitness with their reflections over diagonal hyperplanes will turn out to play an important role in deriving the sets  $\mathbb{A}_k$ , as we shall derive in the second part of the paper.

2. Examples show that  $\mathbb{A}_2$  may extend beyond  $\mathbb{A}_1 \times \mathbb{A}_1$ , and contain points  $(\tau_1, \tau_2) \in \mathbb{T}^2$  for which  $r(\tau_1) \leq 0$  and  $r(\tau_2) > 0$ , or for which  $r(\tau_1) > 0$  and  $r(\tau_2) \leq 0$ . In the first case  $\tau_1 \notin \mathbb{A}_1$ , in the second case  $\tau_2 \notin \mathbb{A}_1$ . This is illustrated by the class of predator-prey models given by the differential equations

$$\begin{cases} \frac{d}{dt}x_1 = x_1(r(\tau_1) + a(\tau_1, \tau_1)x_1 + a(\tau_1, \tau_2)x_2) \\ \frac{d}{dt}x_2 = x_2(r(\tau_2) + a(\tau_2, \tau_1)x_1 + a(\tau_2, \tau_2)x_2) \end{cases}, \quad (5.20)$$

with  $x_1$  denoting the density of the predator population,  $x_2$  the density of the prey population, and with  $r(\tau_1) < 0$ ,  $r(\tau_2) > 0$ , and  $a(\tau_1, \tau_2) > 0$ ,  $a(\tau_2, \tau_1) < 0$  (and  $a(\tau_1, \tau_1) < 0$  and  $a(\tau_2, \tau_2) < 0$ , as usual). Then there exists a globally attracting interior equilibrium if (and only if) the three conditions  $|A(\tau_1, \tau_2)| > 0$ ,  $s_1(\tau_2; \tau_1) > 0$  and  $r(\tau_2) - r(\tau_1) \frac{a(\tau_2, \tau_1)}{a(\tau_1, \tau_1)} > 0$  hold. (In the second part of the paper we shall extend the invasion fitness function in such a way that the third of these three conditions can also be expressed as  $s_1(\tau_1; \tau_2) > 0$ .)

3. Expressions (5.16) above shows that the dimorphic equilibrium densities can be expressed in terms of the functions  $s_1(\tau_1; \cdot)$  and  $s_1(\tau_2; \cdot)$ . The invasion

fitness function  $s_2(\tau_1, \tau_2; \cdot)$  can be expressed in terms of a fraction of determinants of matrices with  $s_1(\tau_1; \cdot)$  and  $s_1(\tau_2; \cdot)$  as coefficients, as (5.18) shows. These properties hold for all equilibrium densities  $\hat{x}_i(\tau_1, \dots, \tau_k)$ ,  $i = 1, \dots, k$ , and functions  $s_k(\tau_1, \dots, \tau_k; \cdot)$  given by (5.9); they will be stated in full generality in Lemmas 5 and 8.

The following Corollary provides a way to construct monomorphic  $c$ -attractors and invasion fitness functions on these attractors.

**Corollary 5.** Let a function  $u : \mathbb{T}^2 \rightarrow \mathbb{R}$  be given such that for all  $\tau \in \mathbb{T}$ :  $u(\tau, \tau) = 0$ . For each  $\tau_1 \in \mathbb{T}$ , let  $u(\tau_1, \cdot) : \mathbb{T} \rightarrow \mathbb{R}$  denote the function that assigns to  $\tau \in \mathbb{T}$  the value  $u(\tau_1, \tau)$ . Let  $A \subset \mathbb{T}$  be a non-empty open set. Then there exists a family of Lotka-Volterra models  $LV_1(\tau)$ ,  $\tau \in \mathbb{T}$ , for single populations such that  $\mathbb{A}_1 = A$ . The family of invasion fitness functions  $\{s_1(\tau; \cdot)\}_{\tau \in \mathbb{A}_1}$  precisely comprises the family of functions  $\{u(\tau, \cdot)\}_{\tau \in A}$ .

The proof of this statement is as follows: Urysohn's Lemma (see e.g. [57]) implies that there exists a continuous function  $r : \mathbb{T} \rightarrow \mathbb{R}$  which is strictly positive on  $A$  and equal to 0 on  $\mathbb{T} \setminus A$ . For  $\tau \in \mathbb{T}$  define the Lotka-Volterra model  $LV_1(\tau)$  by the differential equation  $\frac{d}{dt}x_\tau = x_\tau(r(\tau) - x_\tau)$ . Then  $LV_1(\tau)$  has a  $c$ -attractor  $\langle \tau \rangle$  (with positive density  $r(\tau)$ ) if and only if  $\tau \in A$ . Consequently,  $\mathbb{A}_1 = A$ . Next construct a Lotka-Volterra model for two populations with an interaction function  $a : \mathbb{T}^2 \rightarrow \mathbb{R}$  given by  $a(\tau_1, \tau_2) = \frac{u(\tau_2, \tau_1) - r(\tau_1)}{r(\tau_2)}$ . The invasion function for  $\langle \tau_1 \rangle \in \mathbb{A}_1$  then is  $s_1(\tau_1; \tau_2) = r(\tau_2) + a(\tau_2, \tau_1)r(\tau_1) = u(\tau_1, \tau_2)$ , and the validity of the statement follows.

After invasion of a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k \rangle$  by a mutant population with trait value  $v = \tau_{k+1}$ , the residents and mutants home in on a (possibly unique)  $c$ -attractor for  $LV_{k+1}(\tau_1, \dots, \tau_k, \tau_{k+1})$ , or on a  $c$ -attractor for a  $LV_l(\tau_{i_1}, \dots, \tau_{i_l})$ , with  $\{i_1, \dots, i_l\} \subset \{1, \dots, k+1\}$ . This outcome generically will depend on the trait values of the resident populations as well as that of the mutant population. Unless  $LV_{k+1}(\tau_1, \dots, \tau_k, \tau_{k+1})$  has a unique  $c$ -attractor to which the dynamics after invasion converges, the outcome furthermore depends on the orbit that the residents and mutants follow. This orbit in turn may depend on the specific  $c$ -attractor that became invaded, and on the point on that  $c$ -attractor where the mutants emerged. Outcomes after invasion will be discussed further in section 5.3,

but a first straightforward result can already be mentioned here. Suppose a mutant population with trait value  $\nu$  emerges from a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k \rangle$ . If  $LV_{k+1}(\tau_1, \dots, \tau_k, \nu)$  is permanent, then necessarily the community of residents and mutants eventually will reach a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k, \nu \rangle$ . We shall introduce the following notation for the family of permanent Lotka-Volterra models:

**Notation 7.**  $\mathbb{P}_k = \{ \langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k \mid LV_k(\tau_1, \dots, \tau_k) \text{ is permanent} \}$

An element of  $\mathbb{P}_1$  is called a *protected monomorphism*; an element in  $\mathbb{P}_2$  is called a *protected dimorphism*, and an element in  $\mathbb{P}_3$  is called a *protected trimorphism*. In general an element of  $\mathbb{P}_k$ ,  $k > 1$ , is called *protected polymorphism* or *protected  $k$ -morphism*. An element of  $\mathbb{A}_k \setminus \mathbb{P}_k$  is called an *unprotected polymorphism* or *unprotected  $k$ -morphism*. The characterisation ‘protected’ in protected polymorphism generalises, on the phenotypic level, the notion of protectedness against extinction as it originally was introduced in the literature on evolutionary genetics, see e.g. [45] and [71]. Permanence implies (in general) the existence of a  $c$ -attractor, and therefore (in the case of a Lotka-Volterra community dynamics) of a unique interior rest point (see also e.g. Theorem 13.5.1 in [49]). Later (Corollary 12) we shall derive for a subclass of Lotka-Volterra models that, provided the mutational steps are sufficiently small, permanence is maintained under trait substitutions and evolutionary branching. It then follows for this subclass that an evolutionary path that starts on a monomorphism (which is protected, since obviously  $\mathbb{P}_1 = \mathbb{A}_1$ ) and proceeds by trait substitutions or evolutionary branching, or starts on a polymorphism that under small mutational steps can be reached from a protected polymorphism, is solely composed of protected  $k$ -morphism, for suitable values of  $k$ .

So far we have introduced  $c$ -attractors and invasion fitness functions on these attractors. The invasion fitness function determines whether or not a mutant population is able to invade a resident community attractor. Before we study the consequences of invasion for the community of residents and mutants in detail, we introduce in an informal way additional notions of adaptive dynamics; we do this by focusing on phenotypic trait evolution related to mono-, di- and trimorphisms.

### 5.2.5 Mono-, di- and trimorphisms: first steps towards a generalisation

In this subsection we analyse phenotypic trait evolution related to mono-, di- and trimorphisms. We recall a number of known results (see e.g. [73]), and present some new ones. In doing so we introduce ideas that we shall develop further in forthcoming sections in a more formal manner. The analysis will be based on three types of figures: the Pairwise Invadability Plot (abbreviated to PIP), the Mutual Invadability Plot (or MIP for short), and the Trait Evolution Plot (TEP). For convenience we shall restrict our analysis with respect to dimorphisms to the subset of  $\mathbb{A}_2$  that intersects with  $\mathbb{A}_1 \times \mathbb{A}_1$  (i.e., we restrict ourselves to dimorphisms that are characterised by expression (5.19)).

*Graphical devices: PIP, MIP and TEP*

A PIP for  $s_1$  is simply a sign plot of  $s_1$ . Since  $s_1(\tau; \tau) = 0$  for all  $\tau \in \mathbb{A}_1$ , the main diagonal  $\{(\tau, \tau) | \tau \in \mathbb{A}_1\}$  belongs to the zero set of  $s_1$ . We assume the factorisation

$$s_1(\tau; \nu) = (\nu - \tau)z_1(\tau; \nu), \quad (5.21)$$

with  $z_1$  a function  $\mathbb{A}_1 \times \mathbb{A}_1 \rightarrow \mathbb{R}$  whose zero set has no self-intersection, and which is assumed to change sign at its zero set. The sign pattern in a PIP of a function  $s_1$  thus is determined by the main diagonal and the function  $z_1$ . Figure 5.2 is an example of a PIP.

As our analysis of phenotypic trait evolution will show, the intersection of the zero set of  $z_1$  with the main diagonal in  $\mathbb{A}_1 \times \mathbb{A}_1$  yields the monomorphic singular points for the adaptive dynamics. At such a point a change from a strictly monomorphic to a dimorphic adaptive dynamics may happen, causing the occurrence of a *trait increment*. A trait increment that is locally enduring on the evolutionary timescale is called evolutionary branching. The local adaptive dynamics in a neighbourhood of a monomorphic singular point can be classified, and the generic classification is done in terms of the first and second-order derivatives of the function  $s_1$ , on the assumption that the zero set of  $z_1$  has no self-intersection at the singularity. To avoid intricacies for the adaptive dynamics away from a singularity, we assume no self-intersection of the zero set of  $z_1$  everywhere.



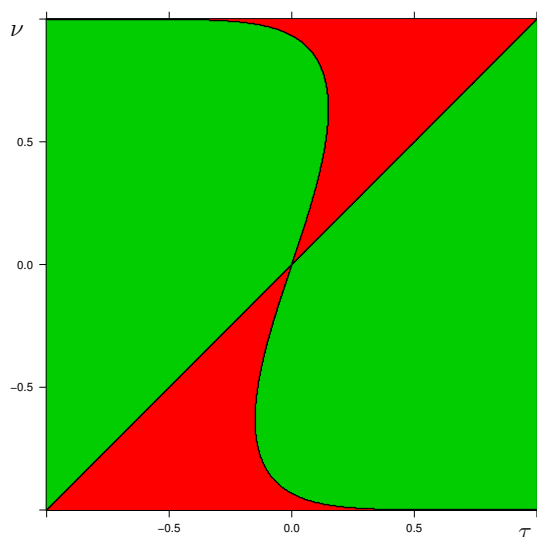


Figure 5.2: PIP for the function

$s_1(\tau; \nu) = 1 - \nu^2 - \frac{e^{-3(\tau-\nu)^2}}{1 - 0.5\nu^2}(1 - 0.5\tau^2)(1 - \tau^2)$  on  $[-1, 1]^2$ . (I.e., the function  $s_1$  is derived from the functions  $r$  and  $a$  as given in Example 1.2). The green region represents positive values, the main diagonal and the black curve represent the zero set of  $s_1$ , and the red region the negative values.

A MIP or Mutual Invasibility Plot for  $s_1$  is a plot that indicates the region of points  $(\tau, \nu) \in \mathbb{A}_1 \times \mathbb{A}_1$  that show mutual invasibility, i.e., it indicates those points  $(\tau, \nu)$  for which both  $s_1(\tau; \nu) > 0$  and  $s_1(\nu; \tau) > 0$  hold good. It is obtained from the PIP of  $s_1$  by taking in this PIP the intersection of the region of points  $(\tau, \nu)$  for which  $s_1(\tau, \nu) > 0$  and its reflection over the main diagonal. As a consequence, the region of mutual invasibility is symmetric under reflection over the main diagonal. Figure 5.1 gives the MIP based on the PIP of Figure 5.2.

A TEP or trait evolution plot for  $s_1$  shows  $\mathbb{A}_1 \times \mathbb{A}_1$ , and within this region  $\mathbb{A}_1$  represented by its embedding in the main diagonal of  $\mathbb{A}_1 \times \mathbb{A}_1$ , as well as the set  $\mathbb{A}_2$ . (From (5.19) it follows that within  $\mathbb{A}_1 \times \mathbb{A}_1$  the set  $\mathbb{A}_2$  is obtained by taking the intersection of the set of mutually invadable points with the collection of points for which the interaction matrix has a positive determinant.) In addition in a TEP the directions of the monomorphic and dimorphic adaptive dynamics are indicated, as well as their rest points and adaptive-dynamical isoclines.

**Remark 6.**

1. By representing  $\mathbb{A}_1$  by its embedding in the main diagonal in  $\mathbb{A}_1 \times \mathbb{A}_1$ , a monomorphic community dynamics parametrised by  $\tau$  is split into a phenotypically equivalent dimorphic dynamics parametrised by  $(\tau, \tau)$ . Although  $(\tau, \nu)$  (with  $\nu$  a mutant of  $\tau$ ) lies close (in a metric sense) to  $(\tau, \tau)$ , the dynamical behaviour of a community parametrised by  $(\tau, \nu)$  generically differs from that of a community parametrised by  $(\tau, \tau)$ : the  $(\tau, \nu)$ -community generically shows competitive exclusion, whereas the  $(\tau, \tau)$ -community exhibits neutral coexistence. The embedding of  $\mathbb{A}_k$  into  $\Delta_{i,k+1}^{k+1}$ ,  $i = 1, \dots, k$  is taken for granted in all studies of adaptive dynamics.
2. To avoid densities from becoming infinite (which is a required constraint in any biologically inspired model involving population densities) it follows from (5.16) that within the region of mutually invadable points no points  $(\tau, \nu)$  are allowed to occur in which the determinant of the interaction matrix  $|A(\tau, \nu)|$  becomes 0. I.e. (by (5.19)), in  $\mathbb{A}_2$  the interaction matrix determinant must be strictly positive.
3. We shall use the following color codes in PIP, MIP and TEP. In a PIP a point  $(\tau_1, \tau_2)$  is coloured red if  $s_1(\tau_1; \tau_2) < 0$ ; it is coloured green in case  $s_1(\tau_1; \tau_2) > 0$ , and black if  $s_1(\tau_1; \tau_2) = 0$ . In a MIP or TEP, a point  $(\tau_1; \tau_2)$  is coloured red if either  $s_1(\tau_1; \tau_2) < 0$  or  $s_1(\tau_2; \tau_1) < 0$ ; it is coloured green if it belongs to  $\mathbb{A}_2$ , and black if either  $s_1(\tau_1; \tau_2) = 0$  or  $s_1(\tau_2; \tau_1) = 0$ . In addition in  $\mathbb{A}_2$  the 1- and 2-isocline (see below) will be represented by a solid and dotted black curve, respectively.

Before we continue with an analysis of the monomorphic and dimorphic adaptive dynamics, we shall first provide an example of a TEP and explain how to read this figure. Figure 5.3 shows the TEP for the function  $s_1$  (i.e., the function that also underlies Figures 5.1 and 5.2). The whole main diagonal corresponds to  $\mathbb{A}_1$ , and the green region represents  $\mathbb{A}_2$ . The main diagonal is divided in two sections by the intersection of the zero set of the function  $z_1$  with the diagonal. The intersection point  $(0, 0)$  (i.e. the diagonal point corresponding to the monomorphic trait value  $\tau = 0$ ) is the rest point for the monomorphic dynamics

(but not necessarily for adaptive dynamics as a whole due to the rare but ongoing occurrence of successful mutants, as in this specific configuration as we shall soon derive), and in the Figure is indicated by the black dot on the main diagonal. The two arrows on the main diagonal indicate the directions of monomorphic adaptive dynamics in these two sections. In the section of points  $(\tau, \tau)$  with  $\tau < 0$  the direction is upwards. Here only a mutant population with trait value  $\nu > \tau$  is able to invade (as follows from the corresponding PIP in Figure 5.2). If such a  $\nu$  is sufficiently close to  $\tau$  then its invasion causes a trait substitution: the density of the mutant population increases and reaches a stable equilibrium on which the resident  $\tau$ -population is replaced by the mutant population. For points  $(\tau, \tau)$  with  $\tau > 0$  the monomorphic direction is downwards: here the  $\tau$ -population gets replaced by an invading mutant population whose trait  $\nu$  is sufficiently close to  $\tau$  and satisfies  $\nu < \tau$ . Monomorphic dynamics for this specific  $s_1$ -function therefore is directed towards the rest point  $\tau = 0$ . Trait values  $\tau$  and  $\nu$  both sufficiently close to 0 which satisfy  $s_1(\tau, \nu) > 0$  and  $s_1(\nu, \tau) > 0$  are mutually invadable. For such  $\tau$  and  $\nu$ , invasion of the monomorphic  $\tau$ -population by the  $\nu$ -mutant population leads to coexistence on the  $c$ -attractor  $\langle \tau, \nu \rangle$ , and results in a trait increment. The adaptive dynamics then leaves  $\mathbb{A}_1$  and enters  $\mathbb{A}_2$ . Once in  $\mathbb{A}_2$ , the dimorphic dynamics is directed away from the monomorphic rest point, as can be seen from the two arrows in  $\mathbb{A}_2$  close to the monomorphic singularity. These arrows indicate the directions of dimorphic dynamics due to mutations in either one of the two traits present at elements of  $\mathbb{A}_2$ . In this specific configuration the direction of trait dynamics sustains on the evolutionary timescale, and evolutionary branching occurs. (How the directions of these arrows can be derived will soon be discussed.)

**Notation 8.** For notational convenience we shall refer to the adaptive dynamics at a point  $(\tau_1, \dots, \tau_k) \in \mathbb{A}_k$  due to only mutations in the  $\tau_i$ -trait as  $i$ -AD.

In  $\mathbb{A}_2$  the two solid curves together form the so-called 1-isocline. The points  $(\tau, \nu)$  on these curves are rest points for the 1-AD, and the 1-AD generically changes direction at the 1-isocline. The dotted curves compose the 2-isocline, and consist of the rest points of the 2-AD, at which 2-AD generically changes direction. The 1- and 2-isoclines divide the part of  $\mathbb{A}_2$  above the main diagonal in four sections,

and in each section the directions of adaptive dynamics due to a mutation in either the  $\tau$ - or  $\nu$ -trait have been indicated. Note that a rest point for the 1-AD or 2-AD generically is not a rest point for the adaptive dynamics as a whole; this is only the case in an intersection point of the 1- and 2-isocline. Rest points for the 1-AD may be locally attracting or repelling for the 1-AD, and a similar statement holds for rest points for the 2-AD. In Figure 5.3 all rest points on the 1-isocline as well as on the 2-isocline are locally attracting for their respective adaptive dynamics. At points within specific regions of either the 1- or the 2-isocline in  $\mathbb{A}_2$  an increment in the number of trait values present may occur due to the entering into  $\mathbb{A}_3$ . Depending on the configuration of the local adaptive dynamics in  $\mathbb{A}_3$ , this may or may not lead to evolutionary branching from  $\mathbb{A}_2$  into  $\mathbb{A}_3$ .

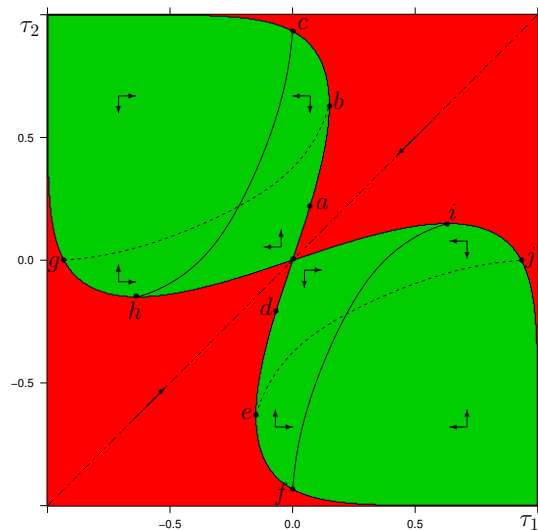


Figure 5.3: The TEP for the function  $s_1(\tau; \nu) = 1 - \nu^2 - \frac{e^{-3(\tau-\nu)^2}}{1 - 0.5\nu^2}(1 - 0.5\tau^2)(1 - \tau^2)$  on  $[-1, 1]^2$ . (The PIP in Figure 5.2 and the MIP in Figure 5.1 are also based on this function  $s_1$ .) The arrows on the main diagonal, i.e.,  $\mathbb{A}_1$ , indicate the direction of monomorphic adaptive dynamics; the arrows in the green region, i.e.  $\mathbb{A}_2$ , indicate the directions of dimorphic dynamics. The solid curves in  $\mathbb{A}_2$  form the 1-isocline, and the dotted curves in  $\mathbb{A}_2$  comprise the 2-isocline. The points  $a$  up to (and including)  $j$  are referred to in the main text.

Due to phenotypic equivalence, the part of  $\mathbb{A}_2$  below the main diagonal yields the same information as the part of  $\mathbb{A}_2$  above the main diagonal. Below the main diagonal, the direction of 2-AD in a point  $(\nu, \tau)$  is equal to the the direction of 1-AD in the point  $(\tau, \nu)$ . E.g., if the 1-AD in  $(\tau, \nu)$  is directed leftwards (causing the decrease of trait value), then in  $(\nu, \tau)$  the 2-AD is directed downwards. A similar statement holds for the direction of 2-AD. As a consequence, the part of the 2-isocline below the main diagonal is obtained by reflection over the main diagonal of the part of the 1-isocline that lies above the main diagonal. Likewise, the part of the 1-isocline below the main diagonal is obtained by reflection over the main diagonal of the part of the 2-isocline that lies above the main diagonal.

We shall now provide more details concerning monomorphic and dimorphic adaptive dynamics, in particular their directions and adaptive-dynamical rest points.

### *Monomorphic dynamics*

Analysis of (5.12) shows that in  $LV(\tau, \nu)$  with  $\nu$  sufficiently close to  $\tau$ , invasion of the monomorphic attractor  $\langle \tau \rangle$  by a mutant population with trait  $\nu$ , i.e., in case  $s_1(\tau; \nu) > 0$ , will cause the ousting of the resident population by the mutant population if in addition  $s_1(\nu; \tau) < 0$  holds. Under these conditions on the evolutionary timescale there thus appears a phenotypic trait substitution from  $\langle \tau \rangle$  to  $\langle \nu \rangle$ , indicated in a TEP by a small arrow going from  $(\tau, \tau)$  to  $(\nu, \nu)$  on the main diagonal. With the assumption of small mutational steps the occurrence of the two inequalities  $s_1(\tau; \nu) > 0$  and  $s_1(\nu; \tau) < 0$  is governed by the sign pattern of the function  $z_1$  in the neighbourhood of the main diagonal element  $(\tau, \tau)$ , which in turn generically is determined by the (monomorphic) invasion fitness gradient

$$\Gamma(\tau) = \partial_{0,1}s_1(\tau; \tau), \quad (5.22)$$

(which equals  $-\partial_{1,0}s_1(\tau; \tau)$ , since  $s_1(\tau; \tau) = 0$  for all  $\tau$ ).<sup>2</sup> In case the invasion gradient is non-zero, the function  $\nu \mapsto s_1(\tau; \nu)$  changes sign at  $\nu = \tau$ , and

<sup>2</sup> For convenience we use the following shorthand notation for derivatives: for a function  $f : \mathbb{R}^k \rightarrow \mathbb{R}$ ,  $f : (x_1, \dots, x_k) \mapsto f(x_1, \dots, x_k)$ , the expression  $\partial_{i_1, \dots, i_k} f(\tau_1, \dots, \tau_k)$  denotes the partial derivative  $\frac{\partial^{i_1 + \dots + i_k}}{\partial x_1^{i_1} \dots \partial x_k^{i_k}} f(x_1, \dots, x_k) \Big|_{(x_1, \dots, x_k) = (\tau_1, \dots, \tau_k)}$ . For derivatives of degree 1 (with respect to the  $i$ -th variable),  $\partial_{0, \dots, 0, 1, 0, \dots, 0} f(\tau_1, \dots, \tau_k)$  may also be denoted as  $\partial_{x_i} f(\tau_1, \dots, \tau_k)$ . (For  $k = 1$ , the usual notation  $f'$  is used for the first derivative of  $f$ , and  $f^{(n)}$  for the  $n$ -th derivative.)

depending on whether the sign of the invasion gradient is negative or positive, a small mutational step will cause the replacement of  $\tau$  by  $\nu < \tau$  or  $\nu > \tau$ . If  $\Gamma(\tau) = 0$ , the trait value  $\tau$  as well as its corresponding  $c$ -attractor are called *singular*, or an *evolutionary singular strategy* (ess). We shall indicate a singular trait value  $\tau$  as  $\tau^*$ . The local behaviour of the function  $\nu \mapsto s_1(\tau^*; \nu)$  in a neighbourhood of an ess  $\tau^*$  is determined by the derivative  $\partial_{0,2}s_1(\tau^*; \tau^*)$ . In case this second-order derivative at a singular trait value is positive,  $s_1(\tau^*; \nu)$  is positive for  $\nu$  sufficiently close to  $\tau^*$ . If in addition also  $\partial_{2,0}s_1(\tau^*; \tau^*) > 0$ , then for values of  $\nu$  sufficiently close to  $\tau^*$  the traits  $\tau^*$  and  $\nu$  are mutually invadable, and also  $|A(\tau^*, \nu)| > 0$  holds. (The latter statement follows from the equality  $|A(\tau, \nu)| = \frac{a(\tau, \tau)}{r(\tau)} \frac{a(\nu, \nu)}{r(\nu)} \left| \begin{pmatrix} 0 & s_1(\tau; \nu) & 1 \\ s_1(\nu; \tau) & 0 & 1 \\ r(\tau) & r(\nu) & 1 \end{pmatrix} \right|$ , which in turn follows from the proof of Lemma 8 below; it also follows from Lemma 9.2 below. This expression also shows that if both  $\tau$  and  $\nu$  belong to  $\mathbb{A}_1$ , and  $(\tau, \nu)$  is such that  $s_1(\tau, \nu) = 0$  as well as  $s_1(\nu, \tau) = 0$ , then  $|A(\tau, \nu)| = 0$ , and  $(\tau, \nu)$  then cannot belong to  $\mathbb{A}_2$ .) Invasion of  $\langle \tau^* \rangle$  by a mutant population with trait value  $\nu$  then will lead to coexistence on the dimorphic attractor  $\langle \tau^*, \nu \rangle \in \mathbb{A}_2$ . If  $\partial_{0,2}s_1(\tau^*; \tau^*) < 0$ , the function  $\nu \mapsto s_1(\tau^*; \nu)$  has a local maximum at  $\nu = \tau^*$ , and  $\langle \tau^* \rangle$  is (at least) locally uninvadable for values  $\nu$  close to  $\tau^*$ . In this case  $\tau^*$  is called a *locally evolutionarily stable strategy* or IESS; in case  $s_1(\tau^*; \nu) < 0$  for any value  $\nu$ ,  $\tau^*$  is an *evolutionarily stable strategy* or ESS.

From the expression

$$s_1(\tau; \nu) = (\nu - \tau)z_1(\tau; \nu), \quad (5.23)$$

with

$$z_1 : \mathbb{T}^2 \rightarrow \mathbb{R}, \quad (5.24)$$

it follows straightforwardly that a trait value  $\tau$  is singular if and only if  $z_1(\tau; \tau) = 0$ , i.e., if and only if  $(\tau, \tau)$  belongs to the intersection of the main diagonal in  $\mathbb{A}_1 \times \mathbb{A}_1$  with the zero set of the function  $z_1$ .

*Dimorphic invasion fitness gradients*

In  $\mathbb{A}_2$  the direction of evolution generically follows from the two dimorphic invasion fitness gradients

$$\Gamma_1(\tau_1, \tau_2) = \partial_{0,0,1}s_2(\tau_1, \tau_2; \tau_1), \quad (5.25)$$

called the 1-invasion fitness gradient at  $\langle \tau_1, \tau_2 \rangle$ , and

$$\Gamma_2(\tau_1, \tau_2) = \partial_{0,0,1}s_2(\tau_1, \tau_2; \tau_2) \quad (5.26)$$

or the 2-invasion fitness gradient at  $\langle \tau_1, \tau_2 \rangle$ . A non-zero value for the 1-invasion fitness gradient determines the direction of evolutionary movement when the mutant population is generated by the resident population carrying trait  $\tau_1$ . In this case, the function  $\nu \mapsto s_2(\tau_1, \tau_2; \nu)$  changes sign at  $\nu = \tau_1$ . If the sign of the 1-invasion fitness gradient is negative, for mutant trait values  $\nu$  sufficiently close to and smaller than  $\tau_1$ ,  $s_2(\tau_1, \tau_2; \nu) > 0$  and  $s_2(\nu, \tau_2; \tau_1) < 0$ . Analysis of (5.1) for  $k = 3$  then again implies that invasion of the mutant population will lead to a replacement of the  $\tau_1$ -population by the mutant population, and evolutionarily the invasion leads to a trait substitution in the first variable, changing  $\langle \tau_1, \tau_2 \rangle$  to  $\langle \nu, \tau_2 \rangle$ . In a TEP this replacement is represented by a small horizontal arrow starting at  $\langle \tau_1, \tau_2 \rangle$  and pointing to the left. A positive sign of the 1-invasion fitness gradient leads to a trait substitution in which the trait in the first variable increases; in a TEP this corresponds to a small horizontal arrow pointing to the right. A similar argument holds for the 2-trait in relation to a non-zero 2-invasion fitness gradient in case the mutants are generated by the  $\tau_2$ -resident population. In a TEP a negative 2-invasion fitness gradient corresponds with a downward pointing arrow, and a positive 2-invasion fitness gradient with an upward pointing arrow. Since we assume rare mutational events and scalar traits, each trait substitution will be in either one of the two possible directions for evolution (and not in both directions simultaneously). Note that in Figure 5.3 invasion of the monomorphic singular trait leads to coexistence of the resident and mutant population on a dimorphic attractor. Since the dimorphic dynamics is directed away from the singularity further into  $\mathbb{A}_2$ , the dimorphic dynamics is locally sustaining, and evolutionary branching occurs.

Generically the 1-invasion fitness gradient changes sign at the 1-isocline

$$I_1 := \{\langle \tau_1, \tau_2 \rangle \in \mathbb{A}_2 \mid \Gamma_1(\tau_1, \tau_2) = 0\}, \quad (5.27)$$

i.e., the collection of  $c$ -attractors  $\langle \tau_1, \tau_2 \rangle$  for which  $\tau_1$  is singular. Likewise, the 2-invasion fitness gradient generically changes sign at the 2-isocline

$$I_2 := \{\langle \tau_1, \tau_2 \rangle \in \mathbb{A}_2 \mid \Gamma_2(\tau_1, \tau_2) = 0\}, \quad (5.28)$$

and for  $\langle \tau_1, \tau_2 \rangle$  on the 2-isocline trait value  $\tau_2$  is singular.

If  $(\tau_1, \tau_2)$  is such that  $s_1(\tau_1; \tau_2) = 0$  and  $s_1(\tau_2; \tau_1) > 0$ , then  $(\tau_1, \tau_2)$  belongs to the boundary of  $\mathbb{A}_2$ .

**Definition 5.** A boundary point  $(\tau_1, \tau_2)$  for  $\mathbb{A}_2$  such that  $s_1(\tau_1; \tau_2) = 0$  and  $s_1(\tau_2; \tau_1) > 0$  is called a *boundary point of  $\mathbb{A}_2$  of the first kind*. A boundary point  $(\tau_1, \tau_2)$  of  $\mathbb{A}_2$  such that  $s_1(\tau_1; \tau_2) > 0$  and  $s_1(\tau_2; \tau_1) = 0$  is called a *boundary point of  $\mathbb{A}_2$  of the second kind*.

A boundary point  $(\tau_1, \tau_2)$  of  $\mathbb{A}_2$  such that both  $s_1(\tau_1; \tau_2) = 0$  and  $s_1(\tau_2; \tau_1) = 0$  is called *degenerate*.

In Figure 5.3, points  $a$  up to  $f$  are boundary points of the first kind, and points  $g$  up to  $j$  are boundary points of the second kind.

By expression (5.17) in a boundary point of the first kind  $s_1(\tau_1, \tau_2; \nu) = s_1(\tau_1; \nu)$ . The point  $(\tau_1, \tau_2)$  then inherits the invasion properties from  $\tau_1$ . (Intuitively, these conclusion are obvious: if the  $\tau_2$ -population cannot invade the environment generated by  $\langle \tau_1 \rangle$ , the attractor  $\langle \tau_1, \tau_2 \rangle$  generates an environment that consists solely of  $\tau_1$ -individuals; the mutants therefore effectively invade a monomorphic  $\langle \tau_1 \rangle$ -attractor. Formally the statement is however not correct at this point in the text, since  $(\tau_1, \tau_2)$  then does not belong to  $\mathbb{A}_2$ , but to its boundary. The function  $s_2 : \mathbb{A}_2 \times \mathbb{T} \rightarrow \mathbb{R}$  can however be extended to such boundary points. The construction of this extension will be discussed in the second part of the paper. The following lines on properties of  $s_2$ , invasion fitness gradients and isoclines have to be read with this extension in mind.). In particular,  $\partial_{0,0,1}s_2(\tau_1, \tau_2; \nu) = \partial_{0,1}s_1(\tau_1; \nu)$ , and consequently  $\Gamma_1(\tau_1, \tau_2) = \Gamma_1(\tau_1)$ , and  $\Gamma_2(\tau_1, \tau_2) = \partial_{0,1}s_1(\tau_1; \tau_2)$ .

In point  $a$ ,  $\Gamma_1(\tau_1, \tau_2) < 0$ , and in point  $d$   $\Gamma_1(\tau_1, \tau_2) > 0$ . From continuity arguments it then follows that for either of these points there exists a



neighbourhood in  $\mathbb{A}_2$  in which the 1-invasion fitness gradient at each point inherits the sign of  $\Gamma(\tau_1)$ . This neighbourhood is bounded by the 1-isocline, and on passing through this isocline the 1-invasion fitness gradient generically switches sign. Furthermore, in  $a$   $\Gamma_2(\tau_1, \tau_2) > 0$ , because the function  $\tau \mapsto s_1(\tau_1; \tau)$  is increasing on a neighbourhood of  $\tau_2$ . (We assume here the absence of the non-generic case of inflection at  $\tau = \tau_2$ .) Similarly,  $(\tau_1, \tau_2)$  then has a neighbourhood in  $\mathbb{A}_2$  in which the 2-isocline is positive, and this neighbourhood is bounded by the 2-isocline. By the same argument, point  $d$  has a neighbourhood in  $\mathbb{A}_2$  in which the 2-isocline is negative.

If a boundary point of the first kind lies 'above' (i.e., in the 2-direction) the monomorphic singular point (points  $c$  and  $f$  in Figure 5.3)  $\Gamma_1(\tau_1, \tau_2)$  necessarily equals 0. Such points therefore belong to (the extension of) the 1-isocline. With respect to mutants generated by the  $\tau_1$ -population,  $(\tau_1, \tau_2)$  inherits the invasion properties from the monomorphic singularity. For the configuration in Figure 5.3, it then follows that points  $c$  and  $f$  are invadable for mutants generated by the  $\tau_1$ -population. (Actually, they are invadable by any mutant population whose trait  $\nu$  satisfies  $\tau_1 < \nu < \tau_2$  (point  $a$ ) or  $\tau_2 < \nu < \tau_1$  (point  $f$ .) Consequently also points  $\langle \tau'_1, \tau'_2 \rangle$  on the 1-isocline sufficiently close to either  $c$  or  $f$ ) are invadable for mutants generated by the  $\tau'_1$ -population. (For a discussion on how isoclines connect to the boundary of  $\mathbb{A}_2$  see also the Appendix in [40].)

If a boundary point of the first kind satisfies  $\partial_{0,1}s_1(\tau_1; \tau_2) = 0$ , then its tangent to the boundary of  $\mathbb{A}_2$  is parallel to the  $\tau_2$ -direction, see points  $b$  and  $e$  in Figure 5.3. In such a point  $\Gamma_2(\tau_1, \tau_2) = 0$ , and it therefore belongs to (the extension of) the 2-isocline. From the local configuration in Figure 5.3 it follows that in points  $b$  and  $e$  the function  $\nu \mapsto s_2(\tau_1, \tau_2; \nu)$  has a local maximum at  $\nu = \tau_2$ . (E.g., in point  $b$  this function equals the function  $\nu \mapsto s_1(\tau_1; \nu)$ , which becomes 0 in  $\nu = \tau_2$ , and for values of  $\nu \neq \tau_2$  sufficiently close to  $\tau_2$   $s_1(\tau_1; \nu) < 0$ .) Consequently, points  $\langle \tau'_1, \tau'_2 \rangle \in \mathbb{A}_2$  on the 2-isocline that are sufficiently close to either  $b$  or  $e$  are uninvadable for mutants generated by the  $\tau'_2$ -population:  $\tau'_2$  then is a IESS for the local 2-AD at  $\langle \tau'_1, \tau'_2 \rangle$ .

In a boundary point of the second kind  $s_2(\tau_1, \tau_2; \nu) = s_2(\tau_2, \tau_1; \nu) = s_1(\tau_2; \nu)$ , and therefore it inherits the invadability properties of  $\tau_2$ . Consequently,  $\Gamma_1(\tau_1, \tau_2) = \partial_{0,1}s_1(\tau_2, \tau_1)$ , and  $\Gamma_2(\tau_1, \tau_2) = \Gamma_1(\tau_2)$ . In Figure 5.3 points  $g$  and  $i$  belong to the

1-isocline and are uninvadable for mutants generated by the  $\tau_1$ -population. In both points the tangent to the boundary of  $\mathbb{A}_2$  is parallel to the  $\tau_1$ -direction. Points  $h$  and  $j$  belong to the 2-isocline, and both are invadable for mutants generated from the  $\tau_2$ -population.

Note that for the configuration shown in Figure 5.3, on the 1-isocline the invasion fitness for mutants generated by the  $\tau_1$ -population at  $\langle \tau_1, \tau_2 \rangle$  changes between the endpoints of the isocline; the same property holds for the invasion fitness of the mutants generated by the  $\tau_2$ -population at  $\tau_1 \tau_2 \rangle$  on the 2-isocline. In the section *Dimorphic and trimorphic dynamics* we shall relate this property to the zero set of the function  $s_2$ .

**Remark 7.** The function  $s_1(\tau_1; \tau_2) = 1 - \tau_2^2 - \frac{e^{-3(\tau_1 - \tau_2)^2}}{1 - 0.5\tau_2^2}(1 - 0.5\tau_1^2)(1 - \tau_1^2)$  on  $[-1, 1]^2$ , for which the TEP in Figure 5.3 is drawn, is such that within the part of  $\mathbb{A}_2$  that lies above the main diagonal in  $\mathbb{A}_1 \times \mathbb{A}_1$ , the 1-isocline connects the boundary point of the first kind above the monomorphic singularity with the boundary point of the second kind in which the tangent to  $\mathbb{A}_2$  is parallel to the  $\tau_2$ -direction. Similarly, the 2-isocline connects the boundary point of the first kind in which the tangent to the boundary of  $\mathbb{A}_2$  is parallel to the  $\tau_1$ -direction with the boundary point of the second kind 'above' the monomorphic singularity. Without further detail we mention here that although the (extensions to the boundary of  $\mathbb{A}_2$  of the) isoclines necessarily pass through these characteristic points, they do not necessarily have to connect these points.

### *Classifying monomorphic singularities*

Under the assumption that  $(\tau, \nu) \mapsto s_1(\tau; \nu)$  is a  $C^2$ -function on a neighbourhood of  $(\tau^*, \tau^*)$ , for a singular trait  $\tau^*$ , we may express  $s_1(\tau; \nu)$  according to its Taylor formula around  $(\tau^*, \tau^*)$ . For notational convenience we shall from now on assume that  $\tau^* = 0$ . By using the notation:

$$s_{i,j} = \frac{1}{i!j!} \partial_{i,j} s_1(0; 0) \quad (5.29)$$

we then may write

$$s_1(\tau; \nu) = s_{1,0}\tau + s_{0,1}\nu + s_{2,0}\tau^2 + s_{1,1}\tau\nu + s_{0,2}\nu^2 + o(\|(\tau, \nu)\|^2) \quad ((\tau, \nu) \rightarrow (0, 0)), \quad (5.30)$$

which, by using the equality  $s_1(\tau; \tau) = 0$ , can be rewritten as

$$s_1(\tau; \nu) = (\nu - \tau)(-s_{2,0}\tau + s_{0,2}\nu + o(\|(\tau, \nu)\|)) \quad ((\tau, \nu) \rightarrow (0, 0)). \quad (5.31)$$

Under the assumption that  $(\tau_1, \tau_2, \nu) \mapsto s_2(\tau_1, \tau_2; \nu)$  is also a  $C^2$ -function on a neighbourhood of  $(0, 0, 0)$ , the consistency conditions  $s_2(\tau_1, \tau_2; \nu) = s_2(\tau_2, \tau_1; \nu)$ ,  $s_2(\tau_1, \tau_2; \tau_1) = 0$ , and  $s_2(0, 0; \nu) = s_1(0; \nu)$  imply that we may write

$$s_2(\tau_1, \tau_2; \nu) = (\nu - \tau_1)(\nu - \tau_2)(s_{0,2} + o(1)) \quad ((\tau_1, \tau_2, \nu) \rightarrow (0, 0, 0)). \quad (5.32)$$

(Such degree of differentiability of  $(\tau_1, \tau_2, \nu) \mapsto s_2(\tau_1, \tau_2; \nu)$  does not have to hold true in general. Away from  $(\tau_1, \tau_2) = (\tau^*, \tau^*)$ , for community-dynamical point attractors the issue is settled by invocation of the inverse function theorem. However, this technique fails in  $(\tau_1, \tau_2) = (\tau^*, \tau^*)$ . In a paper in preparation on bifurcation analysis for adaptive dynamics [54] the first author of the current text derives that for adaptive dynamics for Lotka-Volterra community dynamics, the function  $(\tau_1, \tau_2, \nu) \mapsto s_2(\tau_1, \tau_2; \nu)$  is  $C^{k-2}$  on a neighbourhood of  $(\tau^*, \tau^*, \tau^*)$  if  $(\tau_1, \tau_2) \mapsto s_1(\tau_1; \tau_2)$  is at least  $C^4$  and  $s_{2,0} + s_{0,2} \neq 0$ .) It follows that in a sufficiently small neighbourhood of  $(0, 0)$  the monomorphic fitness gradient at  $\tau$  generically can be approximated by  $-(s_{2,0} - s_{0,2})\tau$ , and the dimorphic 1- and 2-invasion fitness gradients at  $(\tau_1, \tau_2)$  generically can be approximated by  $s_{0,2}(\tau_1 - \tau_2)$  and  $-s_{0,2}(\tau_1 - \tau_2)$ , respectively. The different possible adaptive dynamics in a sufficiently small neighbourhood of an ess generically can be classified in terms of  $s_{2,0}$  and  $s_{0,2}$ , i.e., in case not both derivatives are equal to 0 nor satisfy  $s_{2,0} \pm s_{0,2} = 0$ .

The following classifications for an ess can now be made in terms of  $s_{2,0}$  and  $s_{0,2}$  in case both  $s_{0,2} \neq 0$  and  $s_{2,0} \neq 0$ , and furthermore  $s_{0,2} \pm s_{2,0} \neq 0$  holds, and is graphically presented in Figure 5.4; see also [73] and [16, 18, 39, 70]. (If one of these conditions is not satisfied adaptive dynamics in the neighbourhood of  $(\tau^*, \tau^*)$  depends also on the coefficients of the third-order terms in the Taylor expansion of the function  $(\tau, \nu) \rightarrow s_1(\tau; \nu)$ . The resulting scenarios will be discussed in the paper on bifurcation analysis mentioned above ([54]).) An ess at 0 is a IESS if

$$s_{0,2} < 0. \quad (5.33)$$

An ess at 0 is a convergence stable strategy (i.e., a strategy which is a local attractor for monomorphic trait evolution) if

$$s_{2,0} > s_{0,2}. \quad (5.34)$$

A convergence stable strategy at 0 which is a repeller for dimorphic trait evolution is an Evolutionary Branching Point (EBP). Evolutionary branching occurs if

$$s_{2,0} > s_{0,2} > 0 \quad (5.35)$$

holds. A monomorphic population whose trait value is sufficiently close to  $\tau^*$  then by trait substitutions is driven towards the monomorphic singularity. Sufficiently close to this singularity, invasion of a mutant population will lead to coexistence of the resident and mutant population on a dimorphic  $c$ -attractor. Subsequent trait substitutions will cause the coalition to evolve away from the singularity.

The adaptive dynamics determined by the constraints  $s_{2,0} > -s_{0,2} > 0$  is such that in the dimorphic region a community will be driven towards the narrow end of the coexistence wedge. Eventually the width of the wedge will be sufficiently small for a sufficiently large (but still small) mutational step to push the community over the boundary of the coexistence region, making it monomorphic. The monomorphic evolution which follows is directed towards the ess. A sufficiently large mutation may cause the evolution to become dimorphic again, thereby starting a cyclus of repeated monomorphic and dimorphic evolution close to the singularity, in which the maximum distance to the singularity keeps decreasing.

In case  $s_{2,0}$  and  $s_{0,2}$  are such that  $s_{0,2} > |s_{2,0}|$  the ess is a repeller for monomorphic as well as dimorphic trait evolution. In case  $s_{0,2} > -s_{2,0} > 0$ , a mutational step may push dimorphic evolution over the boundary of the coexistence region into the monomorphic region, thus reducing the number of traits from 2 to 1, at least locally on the evolutionary timescale. This is an example of so-called *evolutionary pruning*. (Note however that the dimorphic evolution cannot have originated from a local evolutionary branching event since the ess is a repeller for the monomorphic dynamics; the dimorphic evolution may be the result of evolutionary pruning that originated in the trimorphic region.)

In all the other cases where there is a region of coexistence attached to the monomorphic singularity, evolution in both the monomorphic as well as the dimorphic case is away from the singularity. Adaptive dynamics thus models the evolutionary process of the regular replacement of phenotypic trait values, possibly interspersed with evolutionary branching and pruning events. In the

latter case, when plotted against evolutionary time the occurring trait values take the characteristic shape of a tree (see Figure 1.1).

**Remark 8.**

1. Note that in i.a. the case that  $\mathbb{A}_2$  is not attached to  $\mathbb{A}_1$  (which is the case if  $s_1$  changes sign everywhere on the main diagonal in  $\mathbb{A}_1 \times \mathbb{A}_1$ , as in the PIP in Figure 5.5), it may occur that a dimorphic coalition by evolutionary dynamics is driven towards the boundary of  $\mathbb{A}_2$ . Close to the boundary a sufficiently large (but still small) mutation may cause the coalition to become monomorphic. Since in this case stepping back from  $\mathbb{A}_1$  into  $\mathbb{A}_2$  cannot happen under small mutational steps, trait evolution will proceed in  $\mathbb{A}_1$ , i.e., evolutionary pruning occurs. In case subsequent mutations in  $\mathbb{A}_2$  drive the adaptive dynamics to the 2-isocline (in the upper left part of  $\mathbb{A}_2$  in Figure 5.5(b)), it depends on the local dynamics at the 2-isocline how the evolutionary process will proceed: a mutation in the 1-trait will bring the dynamics closer to the boundary of  $\mathbb{A}_2$ , and thus to pruning, whereas a mutation in the 2-trait may possibly cause evolutionary branching to occur (although this is excluded in a neighbourhood of either one of the endpoints  $(\tau_1, \tau_2)$  of the 2-isocline, since in such a point  $s_2(\tau_1, \tau_2; \nu) < 0$  for a mutant trait  $\nu$  generated by  $\tau_2$ ).
2. The case where evolution in  $\mathbb{A}_2$  is towards the monomorphic singularity and evolution in  $\mathbb{A}_1$  is away from that singularity requires a TEP that in our framework is excluded by the condition on non-self-intersection of the zero set of the function  $z_1$  in  $(0,0)$ . Figure 5.6 shows a configuration of a TEP that allows for this scenario, with  $s_1(\tau; \nu) = (\nu - \tau)(\nu + 0.8\tau)(\nu + 4\tau)$ . In the left upper part of  $\mathbb{A}_2$ , sufficiently close to the monomorphic singularity a mutation in either the  $\tau_1$ - or  $\tau_2$ -population will cause the community to become monomorphic, and subsequent mutations will cause a dynamics in the upwards direction in  $\mathbb{A}_1$  (possibly first passing through the monomorphic singularity, depending on where the monomorphic dynamics starts). Note that the singularity in this configuration is unstable with respect to small perturbations: generically a small perturbation will result in a dynamics in the neighbourhood of a singularity that resembles one for a non-self-

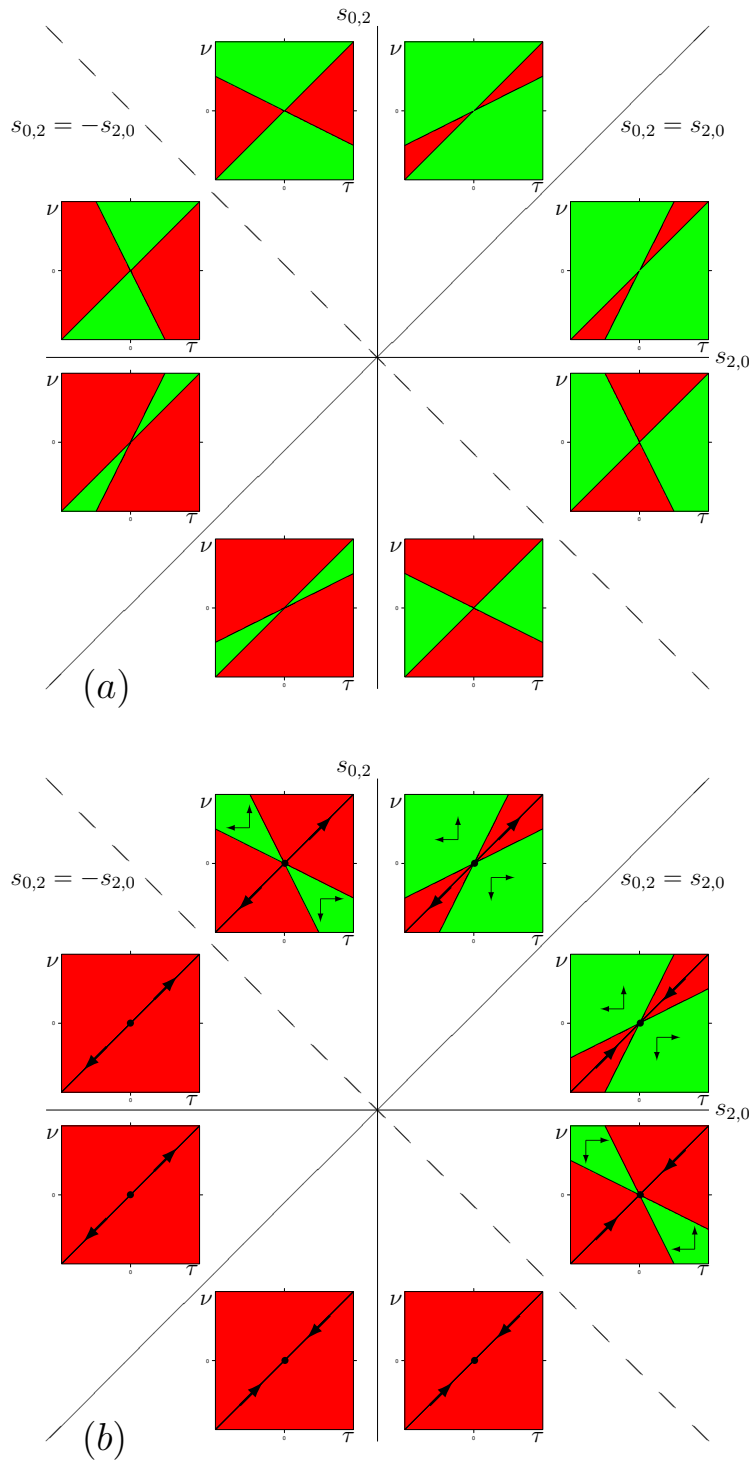


Figure 5.4: The classification of PIPs (a) and TEPS (b) in a sufficiently small neighbourhood of an ess in terms of  $s_{2,0}$  and  $s_{0,2}$  in case both  $s_{2,0} \neq 0$  and  $s_{0,2} \neq 0$ , and furthermore  $s_{2,0} \pm s_{0,2} \neq 0$  holds.

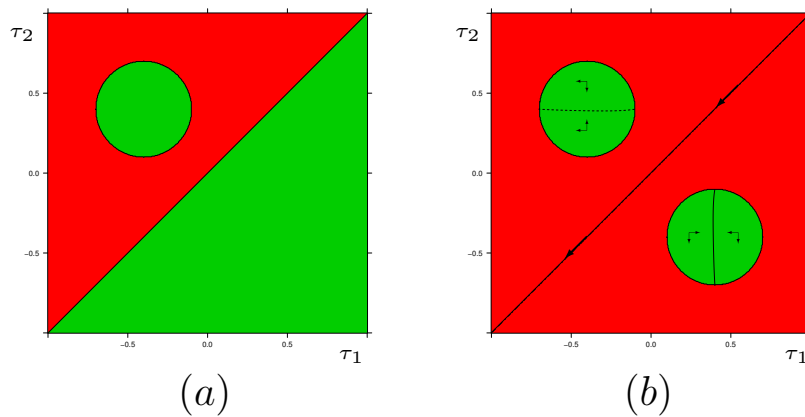


Figure 5.5: Figure (a) shows a PIP, and Figure (b) its corresponding TEP. In the upper left part of  $\mathbb{A}_2$  there is no 1-isocline, and in the lower right part of  $\mathbb{A}_2$  the 2-isocline is absent.

intersecting  $z_1$ . [59] gives an example of an  $\mathbb{A}_2$  attached to  $\mathbb{A}_1$  which allows for evolutionary pruning followed by a monomorphic dynamics evolving towards an ESS.

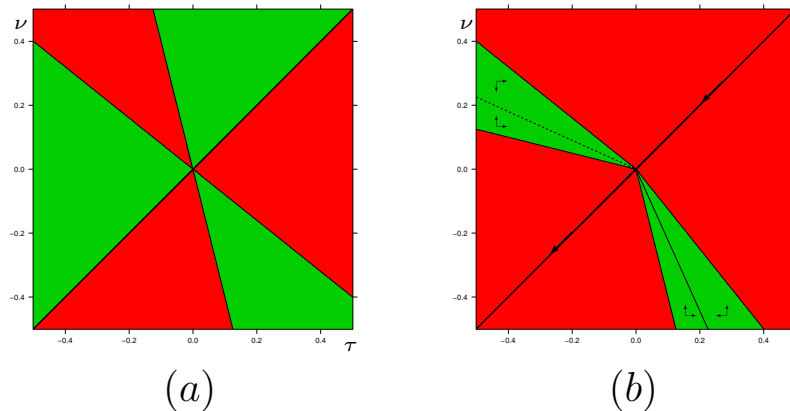


Figure 5.6: Figure (a) shows the PIP for  $s_1(\tau; \nu) = (\nu - \tau)(\nu + 0.8\tau)(\nu + 4\tau)$  on  $[-0.5, 0.5]^2$ , and Figure (b) its corresponding TEP. In the upper left part of  $\mathbb{A}_2$  there is no 1-isocline; equivalently in the lower right part of  $\mathbb{A}_2$  the 2-isocline is absent. The arrows on the main diagonal indicate the direction of the monomorphic dynamics, and the arrows within  $\mathbb{A}_2$  indicate the directions of 1-AD and 2-AD.

Since a TEP is determined by  $z_1$ , which in turn depends on the functions  $r$  and  $a$ , a change of parameters in these functions generically will cause a change in the regions of coexistence. It thus may happen due to a change in parameters that

a coalition goes extinct, or that an IESS turns into an invadable singularity. The evolutionary implications of parameter changes at a monomorphic singularity are studied in the bifurcation analysis paper [54].

### *Dimorphic and trimorphic dynamics*

After this analysis of evolutionary dynamics at a monomorphic singularity we shall now address the topic of adaptive dynamics in  $\mathbb{A}_2$  away from a monomorphic singularity. In particular we are interested in the dynamics in the neighbourhood of a 1- or 2-isocline. Here the possibility may occur that the evolutionary trajectory proceeds by entering the region of trimorphisms. The set  $\mathbb{A}_2$  is symmetric under reflection over the main diagonal in  $\mathbb{A}_1 \times \mathbb{A}_1$ , and therefore we can restrict our attention to dimorphisms  $\langle \tau_1, \tau_2 \rangle \in \mathbb{A}_2 \cap V_{2,\sigma_0}$  (with  $V_{2,\sigma_0}$  as introduced in Notation 1), i.e., to dimorphisms  $\langle \tau_1, \tau_2 \rangle \in \mathbb{A}_2$  for which  $\tau_1 < \tau_2$  holds. For notational convenience we shall indicate the set  $\mathbb{A}_2 \cap V_{2,\sigma_0}$  simply by  $\mathbb{A}_2$ . We assume the factorisation

$$s_2(\tau_1, \tau_2; \nu) = (\nu - \tau_1)(\nu - \tau_2)z_2(\tau_1, \tau_2; \nu), \quad (5.36)$$

with  $z_2(\tau_1, \tau_2; \nu) = z_2(\tau_2, \tau_1; \nu)$ , and the zero set of  $z_2$  again having no self-intersection.

As discussed earlier in this section (under the heading Dimorphic invasion gradients), generically trait evolution in  $\mathbb{A}_2$  is by trait substitutions as determined by the signs of the invasion gradients  $\Gamma_1(\tau_1, \tau_2)$  and  $\Gamma_2(\tau_1, \tau_2)$ , i.e., by the sign pattern of the function  $s_2$  in the  $\nu$ -direction at  $(\tau_1, \tau_2, \tau_1) \in \Delta_{1,3}^3$  and at  $(\tau_1, \tau_2, \tau_2) \in \Delta_{2,3}^3$ . This sign pattern in turn is determined by the function  $z_2$ . For deriving the directions of adaptive dynamics it is thus convenient to embed  $\mathbb{A}_2$  in the two hyperplanes  $\Delta_{1,3}^3$  and  $\Delta_{2,3}^3$ . The factorisation (5.36) implies that

$$\Gamma_1(\tau_1, \tau_2) = \partial_{0,0,1}s_2(\tau_1, \tau_2; \tau_1) = -(\tau_2 - \tau_1)z_2(\tau_1, \tau_2; \tau_1), \quad (5.37)$$

and

$$\Gamma_2(\tau_1, \tau_2) = \partial_{0,0,1}s_2(\tau_1; \tau_2, \tau_2) = (\tau_2 - \tau_1)z_2(\tau_1, \tau_2; \tau_2). \quad (5.38)$$

Therefore, at a point  $(\tau_1, \tau_2, \tau_1) \in \Delta_{1,3}^3$  (with  $\tau_1 < \tau_2$ ) the gradient  $\Gamma_1(\tau_1, \tau_2)$  is positive (negative) if and only if  $z_2(\tau_1, \tau_2; \tau_1)$  is negative (positive). Similarly, at a point  $(\tau_1, \tau_2, \tau_2) \in \Delta_{2,3}^3$  the gradient  $\Gamma_2(\tau_1, \tau_2)$  is positive (negative) if and only



if  $z_2(\tau_1, \tau_2; \tau_2)$  is positive (negative). A trait substitution due to a mutation in the 1-trait then corresponds to a step in the 1-direction (or, more precisely, in the 1,3-direction, i.e., the direction of the vector  $(1,0,1)$  in  $\mathbb{T}^3$ ) in the embedding of  $\mathbb{A}_2$  in  $\Delta_{1,3}^3$ , in a process similar to stepping along the diagonal  $\Delta_{1,2}^2$  due to trait substitutions in the embedded  $\mathbb{A}_1$ . A trait substitution in the 2-trait corresponds to a step in the 2,3- or  $(0,1,1)$ -direction in the embedding of  $\mathbb{A}_2$  in  $\Delta_{2,3}^3$ . The evolutionary path followed by the dimorphic community in  $\mathbb{A}_2$  then can be represented in two ways: in  $\Delta_{1,3}^3$  as well as in  $\Delta_{2,3}^3$ . A trait substitution  $\langle \tau_1, \tau_2 \rangle \rightarrow \langle \tau'_1, \tau_2 \rangle$  is represented in  $\Delta_{1,3}^3$  by stepping from  $(\tau_1, \tau_2, \tau_1)$  to  $(\tau'_1, \tau_2, \tau_1)$ , and in  $\Delta_{2,3}^3$  by stepping from  $(\tau_1, \tau_2, \tau_2)$  to  $(\tau'_1, \tau_2, \tau_2)$ . Similarly, the trait substitution  $\langle \tau_1, \tau_2 \rangle \rightarrow \langle \tau_1, \tau'_2 \rangle$  in  $\Delta_{1,3}^3$  is indicated by the change from  $(\tau_1, \tau_2, \tau_1)$  into  $(\tau_1, \tau'_2, \tau_1)$ , and in  $\Delta_{2,3}^3$  by the change from  $(\tau_1, \tau_2, \tau_2)$  into  $(\tau_1, \tau'_2, \tau_2)$ .

Trait substitutions in the 1-direction in  $\mathbb{A}_2$  come to a halt either by crossing the boundary of  $\mathbb{A}_2$ , or at the 1-isocline  $I_1$ . At the boundary the evolutionary path becomes monomorphic, and proceeds in  $\mathbb{A}_1$ . We focus here at the dynamics locally at the 1-isocline. From (5.37) it follows that the embedding of  $I_1$  in  $\Delta_{1,3}^3$  is obtained as the intersection of the (2-dimensional) zero set of  $z_2$  with the embedding of  $\mathbb{A}_2$  in  $\Delta_{1,3}^3$ ; the embedded 2-isocline  $I_2$  is obtained as the intersection of the zero set of  $z_2$  with the embedding of  $\mathbb{A}_2$  in  $\Delta_{2,3}^3$ . Figure 5.7 illustrates this.

For convenience we shall denote the embedded isocline  $I_1$  in  $\Delta_{1,3}^3$  also as  $I_1$ , the  $I_2$  embedded in  $\Delta_{2,3}^3$  shall simply be denoted as  $I_2$ . Locally at  $(\tau_1, \tau_2, \tau_1) \in I_1$ , the sign of the invasion fitness of a mutant trait  $\nu$  generated by the  $\tau_1$ -population can be read off from the sign pattern of the function  $s_2$  restricted to the 2-dimensional slice

$$C_{1,3}(\tau_1, \tau_2) = \{(\tau_1 + \tau, \tau_2, \tau_1 + \nu) | \tau, \nu \text{ such that } \tau_1 + \tau, \tau_1 + \nu \in \mathbb{T}\} \quad (5.39)$$

attached to the point  $(\tau_1, \tau_2, \tau_1)$ . (Note that the coordinates  $(\tau, \nu)$  form a local coordinate system in this slice, for which the origin  $(0,0)$  coincides with the point of juncture  $(\tau_1, \tau_2, \tau_1)$ .) In this slice the sign pattern of  $s_2$  essentially is a PIP for the function  $\{\tau \in \mathbb{T} | (\tau_1 + \tau, \tau_2) \in \mathbb{A}_2\} \times \mathbb{T} \rightarrow \mathbb{R}$ ,  $(\tau, \nu) \mapsto s_2(\tau_1 + \tau, \tau_2; \tau_1 + \nu)$ , and is determined by the zero set of the restriction of  $z_2$  to the slice. In the slice information on the mutual invadability conditions  $s_2(\tau_1 + \tau, \tau_2; \tau_1 + \nu) > 0$  and  $s_2(\tau_1 + \nu, \tau_2; \tau_1 + \tau) > 0$  can be obtained. In the second part of the paper we shall

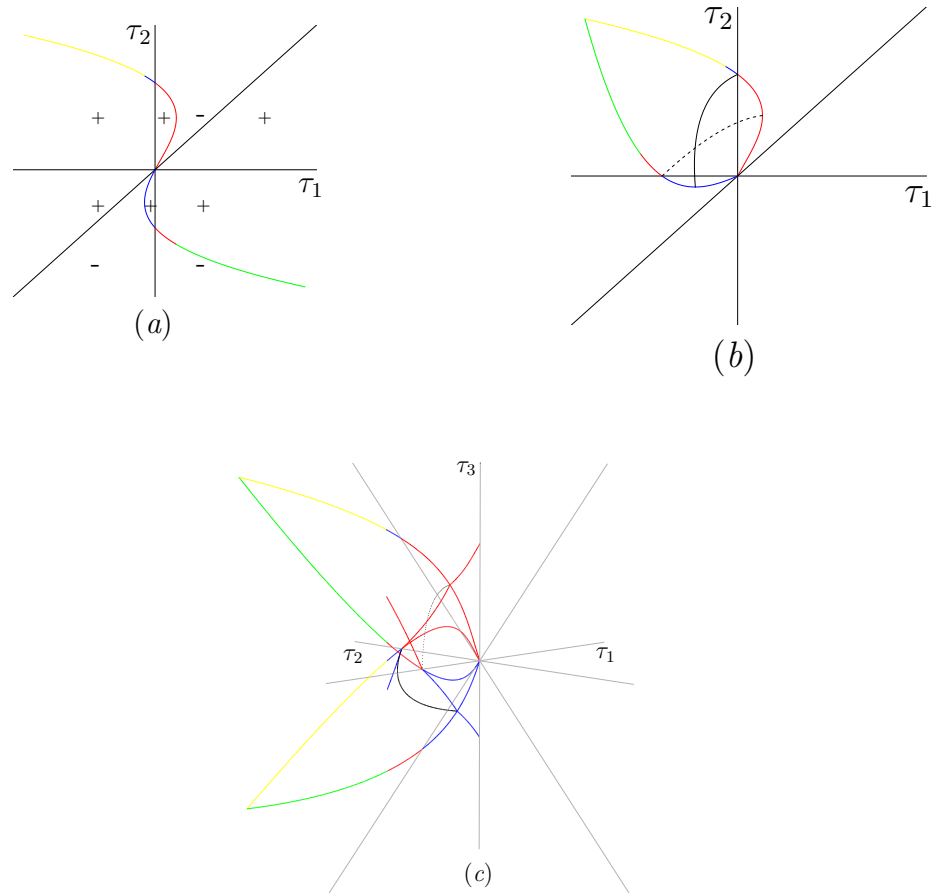


Figure 5.7: Figure (a) shows the zero set of  $z_1$  and the PIP obtained from it. The regions where  $s_1$  is positive are indicated by a + sign, and the regions where  $s_1$  is negative are indicated by a - sign (instead of by green and red regions respectively, as in previous Figures). The zero set has been divided into several coloured parts in such a way that parts of the same color lie above each other with respect to the  $\tau_2$ -direction. Figure (b) shows the TEP obtained from the PIP in Figure (a); the  $\mathbb{A}_2$ -region above the main diagonal is enclosed by the coloured zero sets of the first and second kind. In Figure (c) coloured points  $(\tau_1, \tau_2, \tau_3)$  are indicated that belong to the zero set of  $z_2$  and that satisfy either  $s_1(\tau_1; \tau_2) = 0$  and  $s_1(\tau_1; \tau_3) = 0$ , or  $s_1(\tau_2; \tau_1) = 0$  and  $s_1(\tau_2; \tau_3) = 0$ . Such a point  $(\tau_1, \tau_2, \tau_3)$  inherits the color code from  $(\tau_1, \tau_2)$  as shown in the PIP in Figure (a).  $\mathbb{A}_2$  can be embedded in  $\Delta_{1,3}^3$  and  $\Delta_{2,3}^3$ . The intersection of the zero set of  $z_2$  with these two embeddings yields the 1-isocline in  $\Delta_{1,3}^3$  and the 2-isocline in  $\Delta_{2,3}^3$ .

derive that if  $\langle \tau_1, \tau_2 \rangle$  (not necessarily on the 1-isocline) gets invaded by a mutant  $\nu$  generated by the  $\tau_1$ -population, coexistence on a trimorphism  $\langle \tau_1, \tau_2, \nu \rangle$  requires that the mutual invadability conditions  $s_2(\tau_1, \tau_2; \nu) > 0$  and  $s_2(\nu, \tau_2, \tau_1) > 0$  are being satisfied, but that these conditions are however not a priori sufficient. (In particular, additional information on  $s_2(\tau_1, \nu; \tau_2)$  is needed. Since  $(\tau_1, \nu, \tau_2)$  lies close to  $\Delta_{1,2}^3$ , and  $(\tau_1, \nu)$  generically is not a dimorphic attractor, in the next part of the paper the function  $s_2$  will be extended to  $\Delta_{1,2}^3$  and its neighbourhood in order to give meaning to the expression  $s_2(\tau_1, \nu; \tau_2)$ . More generally we formulate conditions that are required to hold in order that invasion of a  $k$ -morphism  $\langle \tau_1, \dots, \tau_k \rangle$  by a mutant  $\nu$ -population leads to coexistence on the  $k + 1$ -morphism  $\langle \tau_1, \dots, \tau_k, \nu \rangle$ . We then derive that these conditions are satisfied in case  $\langle \tau_1, \dots, \tau_k \rangle$  belongs to one of the isoclines  $I_i = \{(\tau_1, \dots, \tau_k) \mid \partial_{0, \dots, 0, 1} s_k(\tau_1, \dots, \tau_k; \tau_i) = 0\}$ ,  $i = 1, \dots, k$ . The necessary conditions that we derive are however not sufficient to conclude coexistence on the  $k + 1$ -morphism.)

In  $C_{1,3}(\tau_1, \tau_2)$  the points  $(\tau_1 + \tau, \tau_2, \tau_1 + \nu)$  that satisfy the mutual invadability conditions  $s_2(\tau_1 + \tau, \tau_2; \tau_1 + \nu) > 0$  and  $s_2(\tau_1 + \nu, \tau_2; \tau_1 + \tau) > 0$  can be represented by means of the MIP derived from the PIP in this slice. (Note that, due to the possible decentral location of the point  $(\tau_1, \tau_2, \tau_1)$  on the diagonal in  $C_{1,3}(\tau_1, \tau_2)$ , this MIP by construction is restricted to points  $(\tau_1 + \tau, \tau_2, \tau_1 + \nu)$  for which  $\tau$  and  $\nu$  satisfy the following constraint:  $|\tau|, |\nu| \leq \min(|\tau_1 - \min(\mathbb{T})|, |\tau_1 - \max(\mathbb{T})|)$ .) This MIP is bounded by those elements  $(\tau_1 + \tau, \tau_2, \tau_1 + \nu) \in C_{1,3}(\tau_1, \tau_2)$  for which either  $z_2(\tau_1 + \tau, \tau_2; \tau_1 + \nu) = 0$  or  $z_2(\tau_1 + \nu, \tau_2; \tau_1 + \tau) = 0$ . The points in this MIP that represent trimorphic attractors are denoted by  $\mathbb{A}_{1,3}(\tau_1, \tau_2)$ :

$$\mathbb{A}_{1,3}(\tau_1, \tau_2) = C_{1,3}(\tau_1, \tau_2) \cap \mathbb{A}_3. \quad (5.40)$$

Note that  $\mathbb{A}_{1,3}(\tau_1, \tau_2)$  does not necessarily lie close to  $(\tau_1, \tau_2, \tau_1)$ , and may be empty for specific values of  $(\tau_1, \tau_2)$ . The dynamics due to mutations in the 1- and 3-populations in  $\mathbb{A}_{1,3}(\tau_1, \tau_2)$  are restricted to the slice  $C_{1,3}(\tau_1, \tau_2)$ , whereas the dynamics due to mutations in the 2-population is directed perpendicular to the slice. By indicating the directions of the trimorphic evolution within  $\mathbb{A}_{1,3}(\tau_1, \tau_2)$  a TEP is obtained for the restriction of  $s_3$  to  $C_{1,3}(\tau_1, \tau_2)$ . In case  $\mathbb{A}_{1,3}(\tau_1, \tau_2)$  is attached to  $(\tau_1, \tau_2, \tau_1)$ , the resulting TEP can again generically be classified in terms of  $s_{2,0}$  and  $s_{0,2}$ .

With  $\mathbb{A}_{1,3}$  we denote the union of the  $\mathbb{A}_{1,3}(\tau_1, \tau_2)$  for all the  $(\tau_1, \tau_2)$  belonging to  $I_1$ :

$$\mathbb{A}_{1,3} = \bigcup_{(\tau_1, \tau_2) \in I_1} \mathbb{A}_{1,3}(\tau_1, \tau_2). \quad (5.41)$$

In case  $\mathbb{A}_{1,3}$  is attached to  $I_1$  in a 1-singular point from which  $\mathbb{A}_{1,3}$  can be entered by invasion, adaptive dynamics proceeds in  $\mathbb{A}_3$ . In  $\mathbb{A}_3$  there are three directions in which the evolutionary path may proceed. In case the trimorphic dynamics is directed away from the 1-isocline into  $\mathbb{A}_3$ , evolutionary branching from dimorphisms into trimorphisms occurs. Depending on the mutants that occur and the shape of  $\mathbb{A}_3$ , it may however happen that shortly (on the evolutionary timescale) after entering  $\mathbb{A}_3$  subsequent mutations drive the path again out of  $\mathbb{A}_3$  to proceed in  $\mathbb{A}_2$ .

Similar conclusions can be made with respect to the dynamics locally at the 2-isocline  $I_2$ . For invasion of  $\langle \tau_1, \tau_2 \rangle \in I_2$  by a mutant  $\nu$ -population generated by the  $\tau_2$ -population to lead to coexistence on a trimorphism  $\langle \tau_1, \tau_2, \nu \rangle$ , it is required that the mutual invadability conditions  $s_2(\tau_1, \tau_2; \nu) > 0$  and  $s_2(\tau_1, \nu; \tau_2) > 0$  hold. These invadability conditions are again not a priori sufficient. Here in addition information on  $s_2(\tau_2, \nu; \tau_1)$  is required, which is derived from the extension of  $s_2$  to  $\Delta_{1,2}^3$ . To  $\langle \tau_1, \tau_2 \rangle \in I_2$  we attach the slice

$$C_{2,3}(\tau_1, \tau_2) = \{(\tau_1, \tau_2 + \tau, \tau_2 + \nu) \mid \tau, \nu \text{ such that } \tau_1 + \tau, \tau_1 + \nu \in \mathbb{T}\}, \quad (5.42)$$

and by means of the MIP for the restriction of  $s_2$  to this slice the points  $(\tau_1, \tau_2 + \tau, \tau_2 + \nu)$  that satisfy the mutual invadability conditions  $s_2(\tau_1, \tau_2 + \tau; \tau_2 + \nu) > 0$  and  $s_2(\tau_1, \tau_2 + \nu; \tau_2 + \tau) > 0$  can be obtained. This MIP is bounded by the elements  $(\tau_1, \tau_2 + \tau, \tau_2 + \nu)$  for which either  $z_2(\tau_1, \tau_2 + \tau; \tau_2 + \nu) = 0$  or  $z_2(\tau_1, \tau_2 + \nu; \tau_2 + \tau) = 0$  holds. With

$$\mathbb{A}_{2,3}(\tau_1, \tau_2) = C_{2,3}(\tau_1, \tau_2) \cap \mathbb{A}_3 \quad (5.43)$$

we denote the trimorphisms in the slice  $C_{2,3}(\tau_1, \tau_2)$ . Indicating the directions of the dynamics in  $\mathbb{A}_{2,3}(\tau_1, \tau_2)$  yields again a TEP. The direction of the dynamics due to mutations in the 1-population now is perpendicular to the slice; the directions due to mutations in the 2- and 3-populations are confined to  $\mathbb{A}_{2,3}(\tau_2, \tau_3)$ . The set

$$\mathbb{A}_{2,3} = \bigcup_{(\tau_1, \tau_2) \in I_2} \mathbb{A}_{2,3}(\tau_1, \tau_2) \quad (5.44)$$

denotes the union of trimorphisms in the slices attached to the 2-isocline. Note that by following the 1- or the 2-isocline the TEPs in the slices attached to them generically will change, and the resident trait coordinates  $(\tau_1, \tau_2)$  therefore can be considered as a bifurcation parameter for the local adaptive dynamics in the TEPs along these isoclines.

*Properties of  $\mathbb{A}_3$  and  $\mathbb{A}_k, k \geq 4$*

Due to phenotypic equivalence it follows that in  $\mathbb{A}_{1,3}$  we can confine ourselves to those trimorphic attractors  $\langle \tau_1, \tau_2, \tau_3 \rangle$  for which  $\tau_1 < \tau_3$  holds. Similarly, in  $\mathbb{A}_{2,3}$  it is sufficient to assume that  $\tau_3 < \tau_2$ . Together with the restriction  $\tau_1 < \tau_2$  that we adopted earlier with respect to the dimorphic attractors, we conclude that we may take  $\tau_1 < \tau_3 < \tau_2$ . Thus,  $(\tau_1, \tau_2, \tau_3) \in \mathbb{A}_3$  lies above  $(\tau_1, \tau_2, \tau_1) \in \Delta_{1,3}^3$  and below  $(\tau_1, \tau_2, \tau_2) \in \Delta_{2,3}^3$ , with  $\tau_1 < \tau_2$ . We shall now point to some properties of the adaptive dynamics in  $\mathbb{A}_3$  in relation to the geometry of the zero set of  $z_2$ . This discussion is not intended to be exhaustive, nor is it a classification of the possible dynamics that may occur in  $\mathbb{A}_3$ .

The area of trimorphisms  $\mathbb{A}_3$  is composed of two parts, with one part attached to  $\mathbb{A}_2$  along (parts of) the 1-isocline, and the other part attached to  $\mathbb{A}_2$  along (parts of) the 2-isocline. It is composed of the trimorphisms within each of the slices at the elements  $(\tau_1, \tau_2, \tau_1)$  of the 1-isocline in  $\Delta_{1,3}^3$ , and within each of the slices at the elements  $(\tau_1, \tau_2, \tau_2)$  of the 2-isocline in  $\Delta_{2,3}^2$ , respectively. Note that for the trimorphisms  $\langle \tau_1, \tau_2, \tau_3 \rangle$  in the slices attached to the 1-isocline we may, due to the requirement of mutual invadability with respect to  $\tau_1$  and  $\tau_3$ , restrict ourselves to those trimorphisms for which the inequality  $\tau_1 < \tau_3$  holds (besides  $\tau_1 < \tau_2$ ). Likewise we may assume for  $\langle \tau_1, \tau_2, \tau_3 \rangle$  in the slices attached to the 2-isocline that  $\tau_3 < \tau_2$  (and  $\tau_1 < \tau_2$ ). The parts of  $\mathbb{A}_3$  attached to the two isoclines intersect in case a trimorphism in a slice attached to a point of the 1-isocline belongs also to a slice attached to a point of the 2-isocline, and a trimorphism  $\langle \tau_1, \tau_2, \tau_3 \rangle$  in the intersection may be taken to satisfy  $\tau_1 < \tau_2 < \tau_3$ . Within each slice generically the directions of evolutionary dynamics at  $\langle \tau_1, \tau_2, \tau_3 \rangle$  due to a mutation in one of the resident populations can again be derived from these directions at boundary elements  $(\tau_1, \tau_2, \tau_3)$  for which  $s_2(\tau_1, \tau_2; \tau_3) = 0$  (in a way similar to that which

yields information of the directions of dynamics at  $\langle \tau_1, \tau_2 \rangle$  by considering the dynamics at boundary elements of  $\mathbb{A}_2$ ).

Similar to adaptive dynamics in  $\mathbb{A}_1$  and  $\mathbb{A}_2$  as governed by the functions  $s_1$  and  $s_2$ , respectively, trait evolution in  $\mathbb{A}_k$ ,  $k \geq 3$  is derived from the sign pattern of the functions  $s_k : \mathbb{A}_k \times \mathbb{T} \rightarrow \mathbb{R}$ ,  $(\tau_1, \dots, \tau_k, \nu) \mapsto s_k(\tau_1, \dots, \tau_k; \nu)$ . Factorising  $s_k$  by the function  $z_k$  as  $s_k(\tau_1, \dots, \tau_k; \nu) = (\nu - \tau_1) \dots (\nu - \tau_k) z_k(\tau_1, \dots, \tau_k; \nu)$ , we obtain  $k$  isoclines. The  $i$ -isocline is obtained as the intersection of the zero set of  $z_k$  with  $\Delta_{i,k+1}^{k+1}$ , and is the set of  $k$ -morphisms on which the  $i$ -invasion fitness gradient  $\Gamma_i(\tau_1, \dots, \tau_k) = \partial_{0, \dots, 0, 1} s_k(\tau_1, \dots, \tau_k; \tau_i)$  equals 0. To derive the direction of phenotypic trait substitution in  $\mathbb{A}_k$ , we embed  $\mathbb{A}_k$  in the diagonal hyperplanes  $\Delta_{i,k+1}^{k+1}$ . The local sign structures of  $s_k$  at each of these hyperplanes determine the directions of evolution due to mutations in the diverse  $i$ -traits, and mutual invadability of the  $i$ -trait and a mutant it generates is governed by the sign structure of  $s_k$  at the  $i$ -isocline. The evolutionary steps possible at each of the hyperplanes together determine the evolutionary path in  $\mathbb{A}_k$ , and the local structures at the isoclines determine the local conditions for a possible branching into  $\mathbb{A}_{k+1}$ . If the invasion gradients in  $\mathbb{A}_k$  are such that they drive a coalition towards the boundary of  $\mathbb{A}_k$ , then close to this boundary a sufficiently large mutation may cause a trait substitution out of  $\mathbb{A}_k$ , resulting in evolutionary pruning by extinction of one (or more) populations.

The second part of the paper provides for more mathematical detail for these processes. In particular we derive necessary conditions for evolutionary branching to occur. As a first step we therefore generalise the invasion function.

### 5.3 ADAPTIVE DYNAMICS: THE MATHEMATICAL FRAMEWORK

Whereas the previous section could be read as an introduction to adaptive dynamics, with adaptive dynamics based on Lotka-Volterra community dynamics serving as an example to illustrate the concepts introduced, the discussion that follows will become typical for Lotka-Volterra community dynamics.

For  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ , we assume the set of differential equations (5.1) for  $LV_k(\tau_1, \dots, \tau_k)$  now to be defined not solely on  $\mathbb{R}_+^k$  but on the whole of  $\mathbb{R}^k$ . (We maintain however the assumption that the interaction matrix  $A(\tau_1, \dots, \tau_k)$  is a

$B$ -matrix, which guarantees that the orbits of  $LV_k(\tau_1, \dots, \tau_k)$  remain uniformly bounded in  $\mathbb{R}_+^k$ ; outside  $\mathbb{R}_+^k$  orbits may well wander off to infinity.) We then extend the interpretation of the invasion fitness function  $s_k(\tau_1, \dots, \tau_k; \cdot)$  beyond  $(\tau_1, \dots, \tau_k) \in \mathbb{A}_k$  to  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ . By doing so we leave the realm where the notions introduced so far have a biological meaning. This is however not a mathematical exercise on its own, but eventually (see Corollary 7) will have its consequences for the theory of phenotypic trait evolution: by stepping out of the domain of biologically interpretable notions, we shall deduce what characterises these notions (at least in the context of adaptive dynamics with an underlying Lotka-Volterra community dynamics).

### 5.3.1 A generalisation of the invasion function and its consequences

Expression (5.9) for  $s_k(\tau_1, \dots, \tau_k; \nu)$  is not restricted to  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$ , and is well-defined for any  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ . The solution of the  $k$  linear equations  $r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j)x_j = 0, i = 1, \dots, k$ , in this case does not necessarily have to be positive in all its coordinates.

**Notation 9.** Let  $k \geq 1$ . Similar to the case  $(\tau_1, \dots, \tau_k) \in R_{int}(\mathbb{T}^k)$ , we denote for  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  the solution to the  $k$  linear equations  $r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j)x_j = 0, i = 1, \dots, k$ , by  $\hat{x}(\tau_1, \dots, \tau_k) = (\hat{x}_1(\tau_1, \dots, \tau_k), \dots, \hat{x}_k(\tau_1, \dots, \tau_k))$ .

Besides this extension of the notation of  $\hat{x}(\tau_1, \dots, \tau_k)$ , we remind the reader that in Definition 4 we already defined  $\hat{x}(\lambda) = 0$ .

**Definition 6.** For  $k \geq 1$  the function  $s_k : R(\mathbb{T}^k) \times \mathbb{T} \rightarrow \mathbb{R}$  is defined by  $s_k(\tau_1, \dots, \tau_k; \nu) = r(\nu) + \sum_{i=1}^k a(\nu, \tau_i)\hat{x}_i(\tau_1, \dots, \tau_k)$ , with  $\hat{x}(\tau_1, \dots, \tau_k)$  as in Notation 9.

Together with the definition of  $s_0$  (Definition 4), we thus have defined  $s_k : R(\mathbb{T}^k) \times \mathbb{T} \rightarrow \mathbb{R}$  for any  $k \geq 0$ . The mathematical properties of the invasion fitness functions derived in the previous section in case  $k \geq 1$  extend straightforwardly to the functions  $s_k$  for all  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  (with the exception, already mentioned above, that now  $\hat{x}(\tau_1, \dots, \tau_k)$  does not have to

belong to the interior of the community state space). In particular we have for each  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  and for all  $i \in \{1, \dots, k\}$  that  $s_k(\tau_1, \dots, \tau_k; \tau_i) = 0$  (see also Remark 9 below). For any permutation  $\sigma \in \Sigma_k$ :  $s_k(\tau_1, \dots, \tau_k; \nu) = s_k(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}; \nu)$ . Furthermore, for any  $k, l \in \mathbb{N}$ ,  $l \leq k$  and  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  a subset of distinct elements such that  $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in R(\mathbb{T}^{k-l})$ , the notation  $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \nu)$  makes sense.

**Remark 9.** The property that  $s_k(\tau_1, \dots, \tau_k; \tau_i) = 0$  for  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  follows immediately from Definition 6, and not from the proof of the same statement, in Lemma 3, for the case that  $(\tau_1, \dots, \tau_k) \in R_{int}(\mathbb{T}^k)$ . That proof is valid only for orbits  $(x^t)_{t \geq 0}$  restricted to a closed and bounded subset in the interior of  $\mathbb{R}_+^k$ . This confinement does not hold in general in case the state space is taken to be  $\mathbb{R}^k$ .

**Lemma 4.** Let  $k \geq 1$ , and  $l \in \{1, \dots, k\}$ . Let  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ , and let  $\{j_1, \dots, j_l\}$  denote a subset of distinct elements of  $\{1, \dots, k\}$  such that  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in R(\mathbb{T}^{k-l})$ . Suppose that for all  $\alpha = 1, \dots, l$ :  $\hat{x}_{j_\alpha}(\tau_1, \dots, \tau_k) = 0$ , or that for all  $\alpha = 1, \dots, l$ :  $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}) = 0$ . Then

1. if  $l = k$ , then for all  $j = 1, \dots, k$ :  $\hat{x}_j(\tau_1, \dots, \tau_k) = \hat{x}(\lambda) = 0$ ;
2. if  $1 \leq l \leq k - 1$  and  $i \in \{1, \dots, k\} \setminus \{j_1, \dots, j_l\}$ :  

$$\hat{x}_i(\tau_1, \dots, \tau_k) = \hat{x}_i(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l});$$
3.  $s_k(\tau_1, \dots, \tau_k; \nu) = s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \nu)$ .

The statement of this Lemma is a straightforward consequence of the fact that  $\hat{x}(\tau_1, \dots, \tau_k)$  is the unique solution of (5.4), and the definition of the functions  $s_k$  and  $s_{k-l}$ . The third conclusion can be interpreted as being a consequence of reduction by absence, although in the present context the reduced coalition of traits  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})$  does not have to refer to a  $c$ -attractor, but simply to a trait combination for which the function  $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \cdot)$  is defined. Lemma 7, which we state below, places this Lemma in a broader context.

**Example 2.** From expression (5.16) it follows that at a boundary point  $(\tau_1, \tau_2)$  of  $\mathbb{A}_2 \cap (\mathbb{A}_1 \times \mathbb{A}_1)$  for which  $s_1(\tau_1; \tau_2) = 0$  and  $s_1(\tau_2, \tau_1) > 0$ ,  $\hat{x}_1(\tau_1, \tau_2) > 0$  and



$\hat{x}_2(\tau_1, \tau_2) = 0$ . The previous Lemma then implies that at this point  $\hat{x}_2(\tau_1, \tau_2) = \hat{x}(\tau_1)$ , and  $s_2(\tau_1, \tau_2; \nu) = s_1(\tau_1, \nu)$ . The latter equality also follows from (5.17) by substituting  $s_1(\tau_1; \tau_2) = 0$ . A similar statement holds for points  $(\tau_1, \tau_2)$  for which  $s_1(\tau_1; \tau_2) > 0$  and  $s_1(\tau_2; \tau_1) = 0$ . A point  $(\tau'_1, \tau'_2)$  at which both  $s_1(\tau'_1; \tau'_2) = 0$  and  $s_1(\tau'_2; \tau'_1) = 0$  is degenerate: the determinant of the interaction determinant  $A(\tau'_1, \tau'_2)$  equals 0. In case  $\tau'_1 \neq \tau'_2$ , in such a point  $\lim_{(\tau_1, \tau_2) \rightarrow (\tau'_1, \tau'_2)} s_2(\tau_1, \tau_2; \cdot)$  does not exist. This can be seen by approaching  $(\tau'_1, \tau'_2)$  along the boundary points  $(\tau_1, \tau_2)$  for which  $s_1(\tau_1; \tau_2) = 0$  and  $s_1(\tau_2; \tau_1) > 0$ . The limit then equals the function  $s_1(\tau_1; \cdot)$ . Approaching the degeneracy along the boundary points  $(\tau_1, \tau_2)$  for which  $s_1(\tau_1; \tau_2) > 0$  and  $s_1(\tau_2; \tau_1) = 0$  yields as its limit the function  $s_1(\tau_2; \cdot)$ . Similar discontinuities hold at degenerate  $k$ -morphisms for  $k > 2$ , as we shall derive.

The functions  $s_k$  are now further generalised.

**Definition 7.** Let  $k \geq 1$ , and let  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$ ,  $\nu \in \mathbb{T}$ . We define the  $(r, A)$ -invasion fitness matrix of  $LV_k(\tau_1, \dots, \tau_k)$  with regard to  $\nu$  to be the  $(k+1) \times (k+1)$  matrix

$$\begin{pmatrix} a(\tau_1, \tau_1) & a(\tau_1, \tau_2) & \cdot & \cdot & \cdot & a(\tau_1, \tau_k) & r(\tau_1) \\ a(\tau_2, \tau_1) & a(\tau_2, \tau_2) & a(\tau_2, \tau_3) & \cdot & \cdot & a(\tau_2, \tau_k) & r(\tau_2) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & a(\tau_k, \tau_k) & r(\tau_k) \\ a(\nu, \tau_1) & \cdot & \cdot & \cdot & \cdot & a(\nu, \tau_k) & r(\nu) \end{pmatrix}. \quad (5.45)$$

The reason to call this matrix 'invasion fitness matrix' will become clear after Lemma 5.

**Notation 10.** The  $(r, A)$ -invasion fitness matrix of  $LV_k(\tau_1, \dots, \tau_k)$  with regard to  $\nu$  will for short be denoted by  $F_k(\tau_1, \dots, \tau_k; \nu)$ . It may be abbreviated to

$$F_k(\tau; \nu) = \begin{pmatrix} A(\tau) & r(\tau)^T \\ a(\nu, \tau) & r(\nu) \end{pmatrix},$$

with  $\tau$  denoting the vector of trait values  $(\tau_1, \dots, \tau_k)$ ,  $A(\tau)$  the interaction matrix  $A(\tau_1, \dots, \tau_k)$ ,  $r(\tau)^T$  the transpose of the (row)vector  $r(\tau) = (r(\tau_1), \dots, r(\tau_k))$ , and  $a(\nu, \tau)$  the vector  $(a(\nu, \tau_1), \dots, a(\nu, \tau_k))$ .

Invasion fitness matrices are now used to define functions  $S_k$ .

**Definition 8.** Let  $k \geq 1$ . The function  $S_k : \mathbb{T}^k \times \mathbb{T} \rightarrow \mathbb{R}$  is defined as:

$$S_k(\tau_1, \dots, \tau_k; \nu) = |F_k(\tau_1, \dots, \tau_k; \nu)|. \quad (5.46)$$

In addition we define  $S_0 = s_0$ .

Before we proceed with a number of straightforward properties we introduce the following notation.

**Notation 11.** Let  $M$  denote a matrix. With  $M_{(i,j)}$  we denote the matrix obtained from the matrix  $M$  by deleting its  $i$ -th row and  $j$ -th column.

**Corollary 6.** Let  $k \geq 1$ .

1. The functions  $S_k$  inherit the differentiability properties of the functions  $r$  and  $a$ .

2. For all  $\sigma \in \Sigma_k$ :  $S_k(\tau_1, \dots, \tau_k; \nu) = S_k(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}; \nu)$ .

3.

$$S_k(\tau_1, \dots, \tau_k; \nu) = r(\nu)|A(\tau_1, \dots, \tau_k)| - \sum_{i=1}^k a(\nu, \tau_i)S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i). \quad (5.47)$$

4. For each  $i \in \{1, \dots, k\}$ :  $S_k(\tau_1, \dots, \tau_k; \tau_i) = 0$ , and consequently

$$r(\tau_i)|A(\tau_1, \dots, \tau_k)| = \sum_{j=1}^k a(\tau_i, \tau_j)S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_j). \quad (5.48)$$

5. If  $(\tau_1, \dots, \tau_k) \in \Delta^k$ , then for all  $\nu \in \mathbb{T}$ :  $S_k(\tau_1, \dots, \tau_k; \nu) = 0$ .

6. If for all  $i \in \{1, \dots, k\}$ :  $S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i) = 0$ , and for at least one  $j \in \{1, \dots, k\}$ :  $r(\tau_j) \neq 0$ , then  $|A(\tau_1, \dots, \tau_k)| = 0$ , and consequently for all  $\nu \in \mathbb{T}$ :  $S_k(\tau_1, \dots, \tau_k; \nu) = 0$ .

The first two of these statements are trivially obtained. The third one follows from developing  $|F_k(\tau_1, \dots, \tau_k; \nu)|$  with regard to the elements of the  $(k+1)$ -th row, and permuting the rows in the submatrices  $F_{k-1}(\tau_1, \dots, \tau_k; \nu)_{(k+1,i)}$ ,  $i = 1, \dots, k$ , to

bring the  $i$ -th row to the last position without changing the order of the remaining rows. In the fourth statement the first property follows from the fact that in the fitness matrix  $F_k(\tau_1, \dots, \tau_k; \tau_i)$  the  $i$ -th and  $(k+1)$ -th row are identical. The second property then follows from the first one in combination with the third statement. The fifth statement follows from the fact that if  $(\tau_1, \dots, \tau_k) \in \Delta^k$ , the fitness matrix  $F_k(\tau_1, \dots, \tau_k; \nu)$  has at least two identical rows among the first  $k$  rows, for any value of  $\nu \in \mathbb{T}$ . The two properties in the last statement follow from the third and fourth statement.

We now mention several implications of the previous Corollary. The third statement in Corollary 6 implies the following expression for non-trivial equilibrium densities.

**Lemma 5.** Let  $k \geq 1$  and  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ . The solution  $\hat{x}(\tau_1, \dots, \tau_k) = (\hat{x}_1(\tau_1, \dots, \tau_k), \dots, \hat{x}_k(\tau_1, \dots, \tau_k))$  of the  $k$  linear equations

$$r(\tau_i) + \sum_{j=1}^k a(\tau_i, \tau_j)x_j = 0, i = 1, \dots, k,$$

satisfies:

$$\hat{x}_i(\tau_1, \dots, \tau_k) = -\frac{S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)}{|A(\tau_1, \dots, \tau_k)|}. \quad (5.49)$$

Consequently,

1.

$$s_k(\tau_1, \dots, \tau_k; \nu) = r(\nu) - \sum_{i=1}^k a(\nu, \tau_i) \frac{S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)}{|A(\tau_1, \dots, \tau_k)|}. \quad (5.50)$$

2.

$$S_k(\tau_1, \dots, \tau_k; \nu) = |A(\tau_1, \dots, \tau_k)| s_k(\tau_1, \dots, \tau_k; \nu). \quad (5.51)$$

The last expression in this Lemma justifies the name ‘invasion fitness matrix’ for the matrix  $F_k(\tau_1, \dots, \tau_k; \nu)$  on  $R(\mathbb{T}^k)$ , since

$$s_k(\tau_1, \dots, \tau_k; \nu) = \frac{S_k(\tau_1, \dots, \tau_k; \nu)}{|A(\tau_1, \dots, \tau_k)|} = \frac{|F_k(\tau_1, \dots, \tau_k; \nu)|}{|A(\tau_1, \dots, \tau_k)|}. \quad (5.52)$$

As a consequence of expression (5.52) we now can also extend the notion of invasion fitness gradient from  $\mathbb{A}_k$  to  $R(\mathbb{T}^k)$ : for  $(\tau_1, \dots, \tau_k)$ , and for  $i = 1, \dots, k$ ,

the  $i$ -invasion fitness gradient  $\Gamma_i(\tau_1, \dots, \tau_k)$  equals  $\partial_{0, \dots, 0, 1} s_k(\tau_1, \dots, \tau_k; \tau_i)$ . In  $R(\mathbb{T}^k)$ , the  $i$ -isocline then is defined as to consist of those  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  for which  $\Gamma_i(\tau_1, \dots, \tau_k)$  equals 0.

Lemma 5 implies

**Lemma 6.** Let  $k \geq 1$  and let  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ . The equations (5.1) allow for a unique interior rest point in the community state space if and only if

$$\text{for all } i \in \{1, \dots, k\} : \frac{S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)}{|A(\tau_1, \dots, \tau_k)|} < 0. \quad (5.53)$$

In other words, for  $k \geq 1$  the inequalities (5.53) are necessary conditions for  $\langle \tau_1, \dots, \tau_k \rangle$  to belong to  $\mathbb{A}_k$ . Stated for  $k + 1$  instead of  $k$ , this result together with (5.51) has the following implication for phenotypic trait evolution:

**Corollary 7.** Let  $k \geq 1$  and let  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$ . Suppose a mutant population with phenotypic trait value  $\nu = \tau_{k+1}$  emerges from population  $i$  with positive fitness. For invasion of  $\langle \tau_1, \dots, \tau_k \rangle$  to lead to coexistence on a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k, \tau_{k+1} \rangle \in \mathbb{A}_{k+1}$ , the following conditions are necessary:

1. For all  $j = 1, \dots, k$ :  $\frac{S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)}{|A(\tau_1, \dots, \tau_{k+1})|} < 0$ , and therefore, for all  $j = 1, \dots, k$ :  $|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)|$  as well as  $s_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)$  must be unequal to 0, and  $s_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) > 0$  if and only if  $\text{sign}(|A(\tau_1, \dots, \tau_{k+1})|) = -\text{sign}(|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)|)$ ;
2.  $\text{sign}(|A(\tau_1, \dots, \tau_{k+1})|) = -\text{sign}(|A(\tau_1, \dots, \tau_k)|)$ .

Since in the previous Corollary (under the assumption of small mutational steps)  $\text{sign}(|A(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_i)|) = \text{sign}(|A(\tau_1, \dots, \tau_k)|)$ , it follows that for invasion of  $\langle \tau_1, \dots, \tau_k \rangle$  to lead to coexistence on  $\langle \tau_1, \dots, \tau_k, \tau_{k+1} \rangle \in \mathbb{A}_{k+1}$  in particular  $s_k(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_i; \tau_i) > 0$  must hold.

At the end of the first part of this paper we argued that the adaptive-dynamical scenario that occurs due to the generation of mutants by population  $i$  on an attractor  $\langle \tau_1, \dots, \tau_k \rangle$  on the  $i$ -isocline depends on the local configuration of the zero set of the function  $z_k$  at  $(\tau_1, \dots, \tau_k, \tau_i) \in \Delta_{i, k+1}^{k+1}$ . The Corollary shows that necessary conditions for the coexistence of mutants and residents are obtained

from the mutual invasion fitnesses  $s_k(\tau_1, \dots, \tau_k; \tau_{k+1})$  and  $s_k(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j)$  in the  $C_{i,k+1}(\tau_1, \dots, \tau_{k+1})$ -slice. These conditions have to be combined with conditions on the signs of the determinants  $|A(\tau_1, \dots, \tau_{k+1})|$  and  $|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)|$ , and conditions on the signs of the expressions  $s_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)$ , with  $j \in \{1, \dots, k\} \setminus \{i\}$ . For these values of  $j$  the points  $(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)$  as well as  $(\tau_1, \dots, \tau_{k+1})$  lie close to diagonal hyperplanes, on which the determinants become 0 and on which  $s_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)$  is not defined. In the next subsection we shall derive the required signs by means of Lemma 7, that we state after the following Example.

**Example 3.**

1. From expression (5.53) and the assumption that for all  $\tau \in \mathbb{T} : a(\tau, \tau) < 0$  (Assumption 2) it follows that necessary conditions for the existence of an attractor  $\langle \tau_1, \tau_2 \rangle \in \mathbb{A}_2$  are:

$$\frac{s_1(\tau_1; \tau_2)}{|A(\tau_1, \tau_2)|} > 0, \frac{s_1(\tau_2; \tau_1)}{|A(\tau_1, \tau_2)|} > 0. \quad (5.54)$$

With the results from Example 1 these necessary conditions can be sharpened to the following necessary and sufficient ones:

$$s_1(\tau_1; \tau_2) > 0, s_1(\tau_2; \tau_1) > 0 \text{ and } |A(\tau_1, \tau_2)| > 0. \quad (5.55)$$

(By reversing all inequality signs in (5.55), the necessary conditions in (5.54) are also satisfied, but a unique interior unstable equilibrium is obtained rather than an interior attractor.)

2. With Corollary 7 the necessary and sufficient conditions mentioned in Remark 5.2, for the existence of a globally attracting interior equilibrium for a predator-prey model, can now be rewritten as  $|A(\tau_1, \tau_2)| > 0$ ,  $s_1(\tau_2; \tau_1) > 0$  and  $s_1(\tau_2; \tau_1) > 0$ , although the predator dynamics has no  $c$ -attractor.

The following lemma for generalised invasion fitness functions puts the second statement of Lemma 4 in a more general context.

**Lemma 7.**

1. Let  $k \geq 2$ , and let  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ . Let  $l \in \{1, \dots, k-1\}$ , and let  $\{j_1, \dots, j_l\}$  denote a subset of distinct elements of  $\{1, \dots, k\}$  such that  $j_1 < \dots < j_l$  and  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in R(\mathbb{T}^{k-l})$ . Then for all  $i \in \{1, \dots, k\} \setminus \{j_1, \dots, j_l\}$ :

$$\begin{aligned} & |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i) - \\ & |A(\tau_1, \dots, \tau_k)| S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) = \\ & \sum_{\alpha=1}^l (-1)^{j_\alpha-i} |A(\tau_1, \dots, \tau_k)_{(j_\alpha, i)}| S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}). \end{aligned} \quad (5.56)$$

2. Let  $k \geq 1$ , and let  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ . Furthermore, for  $l \in \{1, \dots, k\}$  let  $\{j_1, \dots, j_l\}$  denote a subset of distinct elements of  $\{1, \dots, k\}$  such that  $j_1 < \dots < j_l$  and  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in R(\mathbb{T}^{k-l})$ . Then for all  $\tau_{k+1} \in \mathbb{T}$ :

$$\begin{aligned} & |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - \\ & |A(\tau_1, \dots, \tau_k)| S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{k+1}) = \\ & \sum_{\alpha=1}^l (-1)^{j_\alpha-(k+1)} |A(\tau_1, \dots, \tau_{k+1})_{(j_\alpha, k+1)}| S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}). \end{aligned} \quad (5.57)$$

A proof of this theorem is given in Appendix 5.5.1. If both determinants  $|A(\tau_1, \dots, \tau_k)| \neq 0$  and  $|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \neq 0$ , then it follows from (5.56) that

$$\begin{aligned} & \frac{S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)}{|A(\tau_1, \dots, \tau_k)|} - \frac{S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i)}{|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})|} = \\ & \sum_{\alpha=1}^l (-1)^{j_\alpha-i} \frac{|A(\tau_1, \dots, \tau_k)_{(j_\alpha, i)}|}{|A(\tau_1, \dots, \tau_k)|} \frac{S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha})}{|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})|}, \end{aligned} \quad (5.58)$$

i.e., by (5.49) and (5.52),

$$\hat{x}_i(\tau_1, \dots, \tau_k) = \hat{x}_i(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}) + \sum_{\alpha=1}^l (-1)^{j_\alpha - i - 1} \frac{|A(\tau_1, \dots, \tau_k)_{(j_\alpha, i)}|}{|A(\tau_1, \dots, \tau_k)|} s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}). \quad (5.59)$$

This expression relates the equilibrium density of population  $i$  for the set of equations (5.4) for  $(\tau_1, \dots, \tau_k)$  to that of the same population for the reduced collection  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})$ . We call (5.59) the *closed* relation for  $(\tau_1, \dots, \tau_k)$  and  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})$  with respect to  $i$ .

Similarly we obtain from (5.57) that if  $|A(\tau_1, \dots, \tau_k)| \neq 0$  and  $|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \neq 0$ , then

$$s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) = s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{k+1}) + \sum_{\alpha=1}^l (-1)^{j_\alpha - (k+1)} \frac{|A(\tau_1, \dots, \tau_{k+1})_{(j_\alpha, k+1)}|}{|A(\tau_1, \dots, \tau_k)|} s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}). \quad (5.60)$$

In biological terms this expression relates invasion fitness on a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k \rangle$  to invasion fitness on a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l} \rangle$ . We call (5.60) the *open* relation for  $(\tau_1, \dots, \tau_k)$  and  $(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})$ .

From (5.59) and (5.60) it follows that if (in addition to the two constraints  $|A(\tau_1, \dots, \tau_k)| \neq 0$  and  $|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \neq 0$ ) for each  $\alpha = 1, \dots, l$ :  $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}) = 0$ , then

$$\hat{x}_i(\tau_1, \dots, \tau_k) = \hat{x}_i(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}),$$

and

$$s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) = s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{k+1}),$$

i.e., we obtain the statement of Lemma 4 for this case.

The following lemma generalises expression (5.18); it states how  $s_k$  can be expressed in terms of the function  $s_1$ .

**Lemma 8.** Let  $r$  have isolated zeros. Then  $s_k : R(\mathbb{T}^k) \times \mathbb{T} \rightarrow \mathbb{R}$  satisfies:

$$s_k(\tau_1, \dots, \tau_k; \nu) = \frac{\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & s_1(\tau_1; \nu) \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & s_1(\tau_2; \nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & s_1(\tau_k; \nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix} \right|}{\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & 1 \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & 1 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & 1 \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & 1 \end{pmatrix} \right|}. \quad (5.61)$$

The proof of this Lemma makes use of generalised invasion functions, and will be given in Appendix 5.5.2. (Note that the property of isolated zeros of  $r$  has already been stated in Assumption 1. We mention it here again as a mathematical necessity: if  $r$  is allowed to be identical to 0 on a neighbourhood, then there exists a neighbourhood of  $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$  on which both the numerator and the denominator of (5.61) become equal to 0. In the case of isolated zeros of  $r$ , zero values in numerator and denominator can however be canceled by means of l'Hôpital's argument.)

### 5.3.2 A closer look at the mathematical conditions for coexistence

We now take a closer look at Corollary 7. Let  $k \geq 1$ , and assume that a mutant population with trait value  $\nu = \tau_{k+1}$  is generated by population  $i$ , with trait value  $\tau_i$ , on  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  which belongs to the  $i$ -isocline, i.e.,  $\Gamma_i(\tau_1, \dots, \tau_k) = 0$ . Without loss of generality we may assume that  $i = k$ , and we shall do so here. From Corollary 7 it follows that in case the mutant trait has a positive invasion fitness  $s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) > 0$ , then for invasion to lead to coexistence of the resident populations together with the mutant population on  $\langle \tau_1, \dots, \tau_k, \tau_{k+1} \rangle \in \mathbb{A}_{k+1}$  it is required that



1. for all  $j = 1, \dots, k-1$ :  $\hat{x}_j(\tau_1, \dots, \tau_{k+1}) > 0$ , i.e.

$$\frac{S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)}{|A(\tau_1, \dots, \tau_{k+1})|} < 0; \quad (5.62)$$

- 2.

$$s_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_k; \tau_k) > 0; \quad (5.63)$$

- 3.

$$\text{sign}(|A(\tau_1, \dots, \tau_k, \tau_{k+1})|) = -\text{sign}(|A(\tau_1, \dots, \tau_k)|). \quad (5.64)$$

We shall analyse these requirements in more detail. First we focus on the requirements as expressed by (5.63) and (5.64).

**Lemma 9.**

1. The function  $\mathbb{T}^{k+1} \rightarrow \mathbb{R}$ :  $(\tau_1, \dots, \tau_k, \tau_{k+1}) \mapsto |A(\tau_1, \dots, \tau_k, \tau_{k+1})|$  satisfies  $\partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_k, \tau_k)| = 0$ .
2. Let  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  belong to the  $k$ -isocline, and let a mutant population with trait value  $\nu = \tau_{k+1}$  be generated by population  $k$ . Then the condition  $\partial_{0, \dots, 0, 2} s_k(\tau_1, \dots, \tau_k; \tau_k) + \partial_{0, \dots, 0, 2, 0} s_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) > 0$  implies that for values  $\tau_{k+1}$  sufficiently close to  $\tau_k$ :  

$$\text{sign}(|A(\tau_1, \dots, \tau_k, \tau_{k+1})|) = -\text{sign}(|A(\tau_1, \dots, \tau_k)|).$$

The proof of this Lemma is given in Appendix 5.5.3

It thus follows that if  $\langle \tau_1, \dots, \tau_k \rangle$  lies on the  $i$ -isocline, then the third necessary condition as mentioned in Corollary 7 generically is implied by the mutual invasion condition  $s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) > 0$  and  $s_k(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_i; \tau_i) > 0$ .

We now turn to necessary condition (5.62). Since  $\tau_{k+1}$  lies close to  $\tau_k$ , for  $j \in \{1, \dots, k-1\}$  the point  $(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j)$  lies close to  $\Delta_{k-1, k}^{k+1}$ , on which the numerator of  $\frac{S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)}{|A(\tau_1, \dots, \tau_{k+1})|}$  equals 0 (Corollary 6.5). Also,  $(\tau_1, \dots, \tau_k, \tau_{k+1})$  lies close to  $\Delta_{k, k+1}^{k+1}$ , on which  $|A(\tau_1, \dots, \tau_{k+1})|$  equals 0. We determine the sign of  $\frac{S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)}{|A(\tau_1, \dots, \tau_{k+1})|}$  by applying a l'Hôpital argument to this fraction. By Lemma 9.1 we have that  $\partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_k, \tau_k)| = 0$ .

**Lemma 10.** Let  $j \in \{1, \dots, k-1\}$ . Then  $\partial_{0, \dots, 0, 1, 0} S_k(\tau_1, \dots, \tau_k, \tau_k \setminus \tau_j; \tau_j) = 0$ .

Appendix 5.5.4 gives a proof for this Lemma. Since both  $\partial_{0,\dots,0,1,0}S_k(\tau_1, \dots, \tau_k, \tau_k \setminus \tau_j; \tau_j) = 0$  and  $\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_k, \tau_k)| = 0$  we do not get insight in how  $\frac{S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)}{|A(\tau_1, \dots, \tau_{k+1})|}$  behaves for values of  $\tau_{k+1}$  close to  $\tau_k$ , so we take the second-order derivatives with respect to  $\tau_{k+1}$  at  $\tau_{k+1} = \tau_k$  in numerator and denominator.

**Lemma 11.** Let  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  belong to the  $k$ -isocline.

1. For  $j \in \{1, \dots, k\}$ :

$$\begin{aligned} \text{sign}(\partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k)) = \\ - \text{sign}\left(\left(-1\right)^{j-k} \frac{d|A(\tau_1, \dots, \tau_{k+1})^{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k}\right). \end{aligned} \quad (5.65)$$

2. Let  $j \in \{1, \dots, k-1\}$ . Let in addition

$\partial_{0,\dots,0,2}S_k(\tau_1, \dots, \tau_k; \tau_k) + \partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) > 0$  hold. Then

$$\frac{\partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_k, \tau_k \setminus \tau_j; \tau_j)}{\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_k)|} < 0. \quad (5.66)$$

We prove the statements in this Lemma in Appendix 5.5.5. With this Lemma we can formulate the following Corollary.

**Corollary 8.** Let  $k \geq 1$  and let  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  belong to the  $i$ -isocline. Suppose a mutant population with phenotypic trait value  $v = \tau_{k+1}$  emerges from population  $i$  with positive fitness. If both

$\partial_{0,\dots,0,2,0,\dots,0}S_k(\tau_1, \dots, \tau_{i-1}, \tau_i, \tau_{i+1}, \dots, \tau_k; \tau_i) > 0$  and  $\partial_{0,\dots,0,2}S_k(\tau_1, \dots, \tau_k; \tau_i) > 0$  hold, then for  $\tau_{k+1}$  sufficiently close to  $\tau_i$  the conditions mentioned in Corollary 7 necessary for invasion to lead to coexistence on  $\langle \tau_1, \dots, \tau_k, \tau_{k+1} \rangle \in \mathbb{A}_{k+1}$  are satisfied.

### 5.3.3 Permanence

In this subsection we discuss permanence in the context of adaptive dynamics. We start with the following definition on  $s$ -permanence, inspired by Exercise 13.6.3 in [49].

**Definition 9.** Let  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$ . The Lotka-Volterra community-dynamical system  $LV_k(\tau_1, \dots, \tau_k)$  with uniformly bounded orbits is called  $s$ -permanent if there exists a vector  $p \in \text{int}(\mathbb{R}_+^k)$  (depending on  $(\tau_1, \dots, \tau_k)$ ) such that

$$\sum_{i; x_i=0} p_i(r(\tau_i) + (A(\tau_1, \dots, \tau_k)x)_i) > 0, \quad (5.67)$$

with summation over all boundary rest points  $x$ .

The motivation for introducing the expression  $s$ -permanence for Lotka-Volterra models that satisfy the properties as stated in the previous definition follows from equation (5.68) below.

**Corollary 9.** Let  $LV_k(\tau_1, \dots, \tau_k)$  be  $s$ -permanent. Then  $LV_k(\tau_1, \dots, \tau_k)$  is permanent.

This Corollary follows from Theorem 13.6.1 and Exercise 13.6.3 in [49].

In treating permanence we shall restrict ourselves to so-called fully subregular Lotka-Volterra systems, which are defined as follows.

**Definition 10.** Let  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$ . The Lotka-Volterra community-dynamical system  $LV_k(\tau_1, \dots, \tau_k)$  is called *fully subregular* if for each  $l = 1, \dots, k$  and each subset  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  (with the  $i_1, \dots, i_l$  mutually distinct) the determinant of the principal minor  $A(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$  satisfies  $|A(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})| \neq 0$ .

Assuming that a Lotka-Volterra system is fully subregular guarantees that if, for  $l \in \{1, \dots, k\}$  and  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ , the boundary component  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$  contains a rest point for  $LV_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$ , then this rest point is unique.

For a fully subregular Lotka-Volterra model (with uniformly bounded orbits), the notion of  $s$ -permanence can be expressed in terms of invasion fitness functions as follows:

a fully subregular Lotka-Volterra model  $LV_k(\tau_1, \dots, \tau_k)$  is  $s$ -permanent if there exist  $k$  (or less) positive numbers  $p_1, \dots, p_k$  such that for each  $l \in \{1, \dots, k\}$  and each subset  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  (with mutually distinct elements  $i_1, \dots, i_l$ ) for which  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists, the inequality

$$\sum_{\alpha=1}^l p_{i_\alpha} s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{i_\alpha}) > 0 \tag{5.68}$$

holds.

Since permanence of  $LV_k(\tau_1, \dots, \tau_k)$  implies the existence of a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k \rangle$  and therefore also the existence of a unique interior rest point for  $LV_k(\tau_1, \dots, \tau_k)$ , it follows that for a fully subregular and  $s$ -permanent  $LV_k(\tau_1, \dots, \tau_k)$ , not only all principal minors of  $A(\tau_1, \dots, \tau_k)$  have a non-zero determinant but also  $A(\tau_1, \dots, \tau_k)$  itself.

**Lemma 12.** Let  $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$  be such that  $LV_k(\tau_1, \dots, \tau_k)$  is fully subregular and  $s$ -permanent. Then there exists a neighbourhood  $U$  of  $(\tau_1, \dots, \tau_k)$  such that for each  $(\tau'_1, \dots, \tau'_k) \in U$ ,  $LV_k(\tau'_1, \dots, \tau'_k)$  is fully subregular and  $s$ -permanent.

A proof of this Lemma is given in Appendix 5.5.6

**Corollary 10.** Let  $LV_k(\tau_1, \dots, \tau_k)$  be a fully subregular and  $s$ -permanent Lotka-Volterra model. If  $\partial_{0, \dots, 0, 1} s_k(\tau_1, \dots, \tau_k; \tau_i) \neq 0$ , then for  $\tau_{k+1}$  sufficiently close to  $\tau_i$  and such that  $s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) > 0$ ,  $LV_k(\tau_1, \dots, \tau_{i-1}, \tau_{k+1}, \tau_{i+1}, \dots, \tau_k)$  is fully subregular and  $s$ -permanent.

**Lemma 13.** Let  $LV_k(\tau_1, \dots, \tau_k)$  be fully subregular and  $s$ -permanent. In addition, let  $(\tau_1, \dots, \tau_k)$  belong to the  $i$ -isocline, and let both  $\partial_{0, \dots, 0, 2, 0, \dots, 0} s_k(\tau_1, \dots, \tau_{i-1}, \tau_i, \tau_{i+1}, \dots, \tau_k; \tau_i) > 0$  and  $\partial_{0, \dots, 0, 2} s_k(\tau_1, \dots, \tau_k; \tau_i) > 0$ . Then for  $\tau_{k+1} \in \mathbb{T}$  sufficiently close to  $\tau_i$  and such that  $LV_{k+1}(\tau_1, \dots, \tau_k, \tau_{k+1})$  is fully subregular,  $LV_{k+1}(\tau_1, \dots, \tau_k, \tau_{k+1})$  is  $s$ -permanent.

The assumption that  $LV_{k+1}(\tau_1, \dots, \tau_k, \tau_{k+1})$  is fully subregular is hardly a constraint on the applicability of this lemma. It is being made to guarantee that, for  $\tau_{k+1} \neq \tau_i$ , in particular the determinants  $|A(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{i_1}, \dots, \tau_{i_l})|$ , with

$\{1, \dots, i_l\} \subset \{1, \dots, k+1\} \setminus \{i, k+1\}$ , are non-zero, which generically will be the case. Appendix 5.5.7 gives a proof of this Lemma.

**Corollary 11.** Let  $LV_k(\tau_1, \dots, \tau_k)$  be fully subregular and  $s$ -permanent. In addition, let  $\langle \tau_1, \dots, \tau_k \rangle$  belong to the  $i$ -isocline, and let both  $\partial_{0, \dots, 0, 2, 0, \dots, 0} s_k(\tau_1, \dots, \tau_{i-1}, \tau_i, \tau_{i+1}, \dots, \tau_k; \tau_i) > 0$  and  $\partial_{0, \dots, 0, 2} s_k(\tau_1, \dots, \tau_k; \tau_i) > 0$ . Suppose a mutant population with trait value  $\nu = \tau_{k+1}$  emerges from population  $i$  on  $\langle \tau_1, \dots, \tau_k \rangle$ , with positive fitness. Then for  $\tau_{k+1}$  sufficiently close to  $\tau_i$ , invasion will lead to coexistence on  $\langle \tau_1, \dots, \tau_{k+1} \rangle \in \mathbb{P}_{k+1}$ .

The  $s$ -permanence of a Lotka-Volterra model  $LV_k(\tau_1, \dots, \tau_k)$  does not necessarily imply  $s$ -permanence of a submodel  $LV_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$ , for a  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ , and  $l \in \{1, \dots, k\}$ . As a consequence, evolutionary pruning caused by the invasion of a mutant population does not necessarily maintain  $s$ -permanence.

**Corollary 12.** Consider the collection of Lotka-Volterra models that are fully subregular.

1. An evolutionary path which starts in a trait combination whose corresponding Lotka-Volterra model is  $s$ -permanent and which consists of sufficiently small mutational steps will end in a  $s$ -permanent Lotka-Volterra model.
2. To reach a non- $s$ -permanent Lotka-Volterra model from a  $s$ -permanent Lotka-Volterra model by means of a sequence of mutational steps requires at least one sufficiently large mutational step.

**Remark 10.** Note that the mutational step size required to maintain  $s$ -permanence due to trait substitution by or coexistence with the invading mutant population depends on the resident community, and does not need to hold uniformly for an infinite number of mutational steps.

## 5.4 DISCUSSION

On the previous pages we have analysed scalar phenotypic trait evolution generated by the occurrence of successful mutants in a Lotka-Volterra

community-dynamical system of populations that reside on a  $c$ -attractor. Many of the results obtained depend on the interaction matrix for the Lotka-Volterra community dynamics. We derived necessary conditions that must be satisfied for invasion of  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  by a mutant population with trait value  $\tau_{k+1} \approx \tau_k$  to lead to coexistence on  $\langle \tau_1, \dots, \tau_k, \tau_{k+1} \rangle \in \mathbb{A}_{k+1}$  (Corollary 7) and criteria that guarantee that these conditions are satisfied (Corollary 8). In addition we showed that in the family of fully subregular Lotka-Volterra models, sufficiently small mutational steps maintain permanence. As a consequence, invasion of a  $c$ -attractor  $\langle \tau_1, \dots, \tau_k \rangle$  for a fully subregular and  $s$ -permanent  $L V_k(\tau_1, \dots, \tau_k)$  by a mutant population with trait value  $\tau_{k+1}$  sufficiently close to  $\tau_i$  will lead to a coexistence on  $\langle \tau_1, \dots, \tau_k, \tau_{k+1} \rangle \in \mathbb{P}_{k+1}$  if  $\langle \tau_1, \dots, \tau_k \rangle$  belongs to the  $i$ -isocline and both  $\partial_{0, \dots, 0, 2, 0, \dots, 0} s_k(\tau_1, \dots, \tau_{i-1}, \tau_i, \tau_{i+1}, \dots, \tau_k; \tau_i) > 0$  and  $\partial_{0, \dots, 0, 2} s_k(\tau_1, \dots, \tau_k; \tau_i) > 0$  (Corollary 11).

It must be noted here that the classification of the monomorphic ess is done for infinitesimally small mutational steps. For an ess that allows for evolutionary branching this process will also occur for small mutational steps when the resident community is not present exactly in the ess but near to it. In that case a sufficiently large mutational step allows to step from  $\mathbb{A}_1$  into  $\mathbb{A}_2$ , as follows from Fig. 5.4. Also, evolutionary pruning will occur close to the boundary of  $\mathbb{A}_2$  to which the evolutionary traject approaches in case a sufficiently large mutational step occurs.

In the same vein the necessary conditions for coexistence that have been derived must be understood. As formulated these necessary conditions deal with coexistence of a successful mutant population with the resident populations whose phenotypes belong to an isocline. Generically, coexistence of successful mutants and a resident community will also be possible under slightly modified necessary conditions in case the resident phenotypes are sufficiently close to an isocline. Figure 5.5 illustrates this. From this Figure it will be clear that there are non-singular monomorphic populations and successful mutant populations that can coexist in  $\mathbb{A}_2$ . The necessary conditions for this to occur can be derived from those for coexistence in case a singularity is created by letting the  $\mathbb{A}_2$ -region make an intersection with  $\mathbb{A}_1$ .

Although we restricted ourselves to scalar phenotypic traits, various results also hold for trait vectors. In particular we may in expression (5.61) substitute

trait vectors instead of scalars for the various symbols  $\tau_i$ ,  $i = 1, \dots, k$  and  $\nu$ , and it easily follows that the necessary conditions (5.62), (5.63) and (5.64) must be satisfied for invasion to lead to coexistence of the mutant population with all resident populations in case of trait vectors. Expressions and results that involve differentiation are however restricted to scalar traits. In case of trait vectors the invasion fitness function can be obtained as a matrix expression, and in a sufficiently small neighbourhood of a singular trait vector adaptive-dynamical properties can be characterised in terms of matrix properties, see e.g. [41].

The presented framework for phenotypic trait evolution raises many interesting questions. A main open problem deals with the topological and geometrical structures of the sets  $\mathbb{A}_k$ ,  $k \geq 1$ . For a closed interval  $\mathbb{T}$  the structure of  $\mathbb{A}_1$  and  $\mathbb{A}_2$  can easily be deduced (at least in case of a single singularity; in case the zero set of  $z_1$  consists of several disjoint subsets there will be multiple monomorphic singularities in  $\mathbb{A}_1$  that will lead to more intricate structures for  $\mathbb{A}_2$ ).  $\mathbb{A}_3$  lies "in between"  $\Delta_{1,3}^3$  and  $\Delta_{2,3}^3$ , and generically (for convenience keeping out of mind "isolated"  $\mathbb{A}_3$  configurations similar to the  $\mathbb{A}_2$  configuration as shown in Figure 5.5) is attached to parts of both the 1-isocline embedded in  $\Delta_{1,3}^3$  and the 2-isocline embedded in  $\Delta_{2,3}^3$  in  $\mathbb{T}^3$ . Similar descriptions hold for  $\mathbb{A}_k$ ,  $k \geq 4$ , but a detailed analysis remains to be done.

A second question concerns the representation of the evolutionary path followed by a community, here for simplicity understood to be a community of two populations. Subsequent steps in  $\mathbb{A}_2$  occur due to 1- and 2-AD replacements. A 1-AD replacement is governed by local properties of the invasion fitness function on  $\mathbb{A}_2$  embedded in  $\Delta_{1,3}^3$ , and similarly a 2-AD replacement follows from the local behaviour of this function on  $\mathbb{A}_2$  embedded in  $\Delta_{2,3}^3$ . This implies that the trajectory of the growing evolutionary path (focusing only on replacements for the moment) is determined by what happens in the two diagonal planes, and these two sequences of replacements (due to either 1- or 2-AD replacements) need to be combined to describe the evolutionary path which the community of two populations follows in  $\mathbb{T}^2$ . Defining a new space based on an equivalence relation between  $\mathbb{A}_2 \subset \Delta_{1,3}^3$  and  $\mathbb{A}_2 \subset \Delta_{2,3}^3$  may be a step towards a solution of this problem.

In a forthcoming article [54] a bifurcation analysis for adaptive dynamics based on Lotka-Volterra community dynamics shall be presented. In this text we shall classify bifurcations of adaptive dynamics for singular traits in terms of the coefficients of the underlying community dynamics. This enables the study of possible evolutionary consequences due to changes in community-dynamical parameters.



## 5.5 APPENDICES

Due to the length of various expressions occurring in Appendices 5.6.1 - 5.6.5 and 5.6.7, these Appendices are presented in landscape mode.

### 5.5.1 Proof of Lemma 7

#### 5.5.1.1 Proof of Lemma 7.1

Without loss of generality we can assume that  $j_1 < j_2 < \dots < j_l$ . We start with rewriting the left hand side of expression (5.56) as:

$$|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| |F_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)| - S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) |A(\tau_1, \dots, \tau_k)|. \quad (5.69)$$

In this expression,  $|F_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)|$  equals  $(-1)^{k-i} |F_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k)|$  by making the last row in  $F_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)$  the  $i$ -th one and shifting all subsequent rows one row downward. Also,  $|A(\tau_1, \dots, \tau_k)|$  equals  $(-1)^{k-i} |A(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)|$  by shifting the  $i$ -th column in  $A(\tau_1, \dots, \tau_k)$  to make it the last one. Multiplying the last column in  $F_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k)$  with  $|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})|$ , and multiplying the last column in  $A(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)$  with  $S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i)$ , yields that (5.69) equals

$$(-1)^{k-i} \times \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & a(\tau_1, \tau_{i-1}) & a(\tau_1, \tau_{i+1}) & \cdot & a(\tau_1, \tau_k) & r(\tau_1) |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_j, \tau_1) & \cdot & a(\tau_j, \tau_{i-1}) & a(\tau_j, \tau_{i+1}) & \cdot & a(\tau_j, \tau_k) & r(\tau_j) |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & a(\tau_k, \tau_{i-1}) & a(\tau_k, \tau_{i+1}) & \cdot & a(\tau_k, \tau_k) & r(\tau_k) |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \end{pmatrix} \right| -$$

$$(-1)^{k-i} \times \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & a(\tau_1, \tau_{i-1}) & a(\tau_1, \tau_{i+1}) & \cdot & a(\tau_1, \tau_k) & S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) \times a(\tau_1, \tau_i) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_j, \tau_1) & \cdot & a(\tau_j, \tau_{i-1}) & a(\tau_j, \tau_{i+1}) & \cdot & a(\tau_j, \tau_k) & S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) \times a(\tau_j, \tau_i) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & a(\tau_k, \tau_{i-1}) & a(\tau_k, \tau_{i+1}) & \cdot & a(\tau_k, \tau_k) & S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) \times a(\tau_k, \tau_i) \end{pmatrix} \right| =$$

$$(-1)^{k-i} \times \begin{pmatrix} a(\tau_1, \tau_1) \cdot a(\tau_1, \tau_{i-1}) \cdot a(\tau_1, \tau_{i+1}) \cdot a(\tau_1, \tau_k) & r(\tau_1) |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| - a(\tau_1, \tau_i) \times S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) \\ \cdot & \cdot \\ a(\tau_j, \tau_1) \cdot a(\tau_j, \tau_{i-1}) \cdot a(\tau_j, \tau_{i+1}) \cdot a(\tau_j, \tau_k) & r(\tau_j) |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| - a(\tau_j, \tau_i) \times S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) \\ \cdot & \cdot \\ a(\tau_k, \tau_1) \cdot a(\tau_k, \tau_{i-1}) \cdot a(\tau_k, \tau_{i+1}) \cdot a(\tau_k, \tau_k) & r(\tau_k) |A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| - a(\tau_k, \tau_i) \times S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_i; \tau_i) \end{pmatrix}.$$

In the last column in the matrix in this expression, the element in the  $j$ -th row by means of (5.47) equals

$$S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_j) + \sum_{\substack{\alpha=1 \\ \alpha \neq j_1, \dots, j_l, i}}^k a(\tau_j, \tau_\alpha) S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_\alpha; \tau_\alpha),$$

and so the previous expression equals

$$(-1)^{k-i} \times \begin{pmatrix} a(\tau_1, \tau_1) \cdot a(\tau_1, \tau_{i-1}) & a(\tau_1, \tau_{i+1}) \cdot a(\tau_1, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_1) + \sum_{\substack{\alpha=1 \\ \alpha \neq j_1, \dots, j_l, i}}^k (a(\tau_1, \tau_\alpha) \times S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_\alpha; \tau_\alpha)) \\ \cdot & \cdot & \cdot \\ a(\tau_j, \tau_1) \cdot a(\tau_j, \tau_{i-1}) & a(\tau_j, \tau_{i+1}) \cdot a(\tau_j, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_j) + \sum_{\substack{\alpha=1 \\ \alpha \neq j_1, \dots, j_l, i}}^k (a(\tau_j, \tau_\alpha) \times S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_\alpha; \tau_\alpha)) \\ \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) \cdot a(\tau_k, \tau_{i-1}) & a(\tau_k, \tau_{i+1}) \cdot a(\tau_k, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_k) + \sum_{\substack{\alpha=1 \\ \alpha \neq j_1, \dots, j_l, i}}^k (a(\tau_k, \tau_\alpha) \times S_{k-l-1}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}, \tau_\alpha; \tau_\alpha)) \end{pmatrix}.$$

In the last column in the matrix of this expression, the summation in each row contributes the same linear combination of corresponding row elements of other columns, and therefore does not affect the determinant. We thus obtain that the expression is equal to

$$(-1)^{k-i} \times \left| \begin{array}{cccccc} a(\tau_1, \tau_1) & \cdot & a(\tau_1, \tau_{i-1}) & a(\tau_1, \tau_{i+1}) & \cdot & a(\tau_1, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_1) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_j, \tau_1) & \cdot & a(\tau_j, \tau_{i-1}) & a(\tau_j, \tau_{i+1}) & \cdot & a(\tau_j, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_j) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & a(\tau_k, \tau_{i-1}) & a(\tau_k, \tau_{i+1}) & \cdot & a(\tau_k, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_k) \end{array} \right|.$$

In the matrix of the expression thus obtained, in the last column  $S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_j)$  equals 0 in case  $j \notin \{j_1, \dots, j_l\}$ . The expression itself therefore is equal to

$$(-1)^{k-i} \times \left( \begin{array}{ccccccc}
a(\tau_1, \tau_1) & \cdot & \cdot & a(\tau_1, \tau_{i-1}) & a(\tau_1, \tau_{i+1}) & \cdot & \cdot & a(\tau_1, \tau_k) & 0 \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
a(\tau_{j_1}, \tau_1) & \cdot & \cdot & a(\tau_{j_1}, \tau_{i-1}) & a(\tau_{j_1}, \tau_{i+1}) & \cdot & \cdot & a(\tau_{j_1}, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_1}) \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
a(\tau_{j_m}, \tau_1) & \cdot & \cdot & a(\tau_{j_m}, \tau_{i-1}) & a(\tau_{j_m}, \tau_{i+1}) & \cdot & \cdot & a(\tau_{j_m}, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_m}) \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
a(\tau_i, \tau_1) & \cdot & \cdot & a(\tau_i, \tau_{i-1}) & a(\tau_i, \tau_{i+1}) & \cdot & \cdot & a(\tau_i, \tau_k) & 0 \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
a(\tau_{j_{m+1}}, \tau_1) & \cdot & \cdot & a(\tau_{j_{m+1}}, \tau_{i-1}) & a(\tau_{j_{m+1}}, \tau_{i+1}) & \cdot & \cdot & a(\tau_{j_{m+1}}, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_{m+1}}) \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
a(\tau_{j_l}, \tau_1) & \cdot & \cdot & a(\tau_{j_l}, \tau_{i-1}) & a(\tau_{j_l}, \tau_{i+1}) & \cdot & \cdot & a(\tau_{j_l}, \tau_k) & S_{k-l}(\tau_1, \dots, \tau_k \setminus \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_l}) \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
a(\tau_k, \tau_1) & \cdot & \cdot & a(\tau_k, \tau_{i-1}) & a(\tau_k, \tau_{i+1}) & \cdot & \cdot & a(\tau_k, \tau_k) & 0
\end{array} \right) =$$

$$(-1)^{k-i} \sum_{\alpha=1}^l (-1)^{j_\alpha+k} S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}) \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & \cdot & a(\tau_1, \tau_{i-1}) & a(\tau_1, \tau_{i+1}) & \cdot & \cdot & a(\tau_1, \tau_k) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_{j_\alpha-1}, \tau_1) & \cdot & \cdot & a(\tau_{j_\alpha-1}, \tau_{i-1}) & a(\tau_{j_\alpha-1}, \tau_{i+1}) & \cdot & \cdot & a(\tau_{j_\alpha-1}, \tau_k) \\ a(\tau_{j_\alpha+1}, \tau_1) & \cdot & \cdot & a(\tau_{j_\alpha+1}, \tau_{i-1}) & a(\tau_{j_\alpha+1}, \tau_{i+1}) & \cdot & \cdot & a(\tau_{j_\alpha+1}, \tau_k) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & \cdot & a(\tau_k, \tau_{i-1}) & a(\tau_k, \tau_{i+1}) & \cdot & \cdot & a(\tau_k, \tau_k) \end{pmatrix} \right| =$$

$\sum_{\alpha=1}^l (-1)^{j_\alpha-i} S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\alpha}) |A(\tau_1, \dots, \tau_k)_{(j_\alpha, i)}|$ , which completes the proof of Lemma 7.1.



5.5.1.2 Proof of Lemma 7.2

To prove the validity of expression (5.57) we rewrite its left hand side as

$$|A(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l})| \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & \cdot & a(\tau_1, \tau_k) & r(\tau_1) \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & \cdot & a(\tau_k, \tau_k) & r(\tau_k) \\ a(\tau_{k+1}, \tau_1) & \cdot & \cdot & a(\tau_{k+1}, \tau_k) & r(\tau_{k+1}) \end{pmatrix} \right| -$$

$$S_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{k+1}) \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & \cdot & a(\tau_1, \tau_k) & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_k, \tau_1) & \cdot & \cdot & a(\tau_k, \tau_k) & 0 \\ a(\tau_{k+1}, \tau_1) & \cdot & \cdot & a(\tau_{k+1}, \tau_k) & 1 \end{pmatrix} \right|$$

and continue in a manner similar as that in the proof of the first statement.

## 5.5.2 Proof of Lemma 8

The denominator in the right hand side of expression (5.61),  $\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & 1 \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & 1 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & 1 \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & 1 \end{pmatrix} \right|$ , can be rewritten by

subtracting the last row from each of the other rows in the matrix. This yields the following determinant:

$$\left| \begin{pmatrix} -r(\tau_1) & s_1(\tau_1; \tau_2) - r(\tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) - r(\tau_k) \\ s_1(\tau_2; \tau_1) - r(\tau_1) & -r(\tau_2) & \cdot & \cdot & s_1(\tau_2; \tau_k) - r(\tau_k) \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) - r(\tau_1) & s_1(\tau_k; \tau_2) - r(\tau_2) & \cdot & \cdot & -r(\tau_k) \end{pmatrix} \right|. \text{ Since, by Definition 6, } s_1(\tau; \nu) = r(\nu) - r(\tau) \frac{a(\nu, \tau)}{a(\tau, \tau)}, \text{ the}$$

previous determinant is equal to

$$\left| \begin{pmatrix} -r(\tau_1) & -a(\tau_2, \tau_1) \frac{r(\tau_1)}{a(\tau_1, \tau_1)} & \cdot & \cdot & -a(\tau_k, \tau_1) \frac{r(\tau_1)}{a(\tau_1, \tau_1)} \\ -a(\tau_1, \tau_2) \frac{r(\tau_2)}{a(\tau_2, \tau_2)} & -r(\tau_2) & \cdot & \cdot & -a(\tau_k, \tau_2) \frac{r(\tau_2)}{a(\tau_2, \tau_2)} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ -a(\tau_1, \tau_k) \frac{r(\tau_k)}{a(\tau_k, \tau_k)} & -a(\tau_2, \tau_k) \frac{r(\tau_k)}{a(\tau_k, \tau_k)} & \cdot & \cdot & -r(\tau_k) \end{pmatrix} \right| = (-1)^k |A(\tau_1, \dots, \tau_k)| \prod_{i=1}^k \frac{r(\tau_i)}{a(\tau_i, \tau_i)}. \quad (5.70)$$

Next we show that the numerator of the right hand side of (5.61) is equal to  $(-1)^k S_k(\tau_1, \dots, \tau_k; \nu) \prod_{i=1}^k \frac{r(\tau_i)}{a(\tau_i, \tau_i)}$ . This is done by means of induction on  $k$ .

For  $k = 1$  we have  $\left| \begin{pmatrix} 0 & s_1(\tau_1; \nu) \\ r(\tau_1) & r(\nu) \end{pmatrix} \right| = -r(\tau_1)s_1(\tau_1; \nu) = -\frac{r(\tau_1)}{a(\tau_1, \tau_1)} S_1(\tau_1; \nu)$ , since by (5.51)  $S_1(\tau_1; \nu) = a(\tau_1, \tau_1)s_1(\tau_1; \nu)$ . The induction hypothesis states that

$$\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_{k-1}) & s_1(\tau_1; \nu) \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_{k-1}) & s_1(\tau_2; \nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_{k-1}; \tau_1) & s_1(\tau_{k-1}; \tau_2) & \cdot & \cdot & 0 & s_1(\tau_{k-1}; \nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_{k-1}) & r(\nu) \end{pmatrix} \right| = (-1)^{k-1} S_{k-1}(\tau_1, \dots, \tau_{k-1}; \nu) \prod_{i=1}^{k-1} \frac{r(\tau_i)}{a(\tau_i, \tau_i)}.$$

The numerator of (5.61),  $\left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & s_1(\tau_1; \nu) \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & s_1(\tau_2; \nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & s_1(\tau_k; \nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix} \right|$ , then is equal to

$$\begin{aligned}
 & \left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & r(\nu) - a(\nu, \tau_1) \frac{r(\tau_1)}{a(\tau_1, \tau_1)} \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & r(\nu) - a(\nu, \tau_2) \frac{r(\tau_2)}{a(\tau_2, \tau_2)} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & r(\nu) - a(\nu, \tau_k) \frac{r(\tau_k)}{a(\tau_k, \tau_k)} \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix} \right| = \\
 & \left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & r(\nu) \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & r(\nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & r(\nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix} \right| + \left| \begin{pmatrix} 0 & s_1(\tau_1; \tau_2) & \cdot & \cdot & s_1(\tau_1; \tau_k) & -a(\nu, \tau_1) \frac{r(\tau_1)}{a(\tau_1, \tau_1)} \\ s_1(\tau_2; \tau_1) & 0 & \cdot & \cdot & s_1(\tau_2; \tau_k) & -a(\nu, \tau_2) \frac{r(\tau_2)}{a(\tau_2, \tau_2)} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k; \tau_1) & s_1(\tau_k; \tau_2) & \cdot & \cdot & 0 & -a(\nu, \tau_k) \frac{r(\tau_k)}{a(\tau_k, \tau_k)} \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & 0 \end{pmatrix} \right|. \quad (5.71)
 \end{aligned}$$

The first of the last two determinants equals  $r(\nu) \times$  (the denominator), and therefore by (5.70) is equal to

$(-1)^k r(\nu) |A(\tau_1, \dots, \tau_k)| \prod_{i=1}^k \frac{r(\tau_i)}{a(\tau_i, \tau_i)}$ . The second determinant in the last expression by the induction hypothesis equals

$$\sum_{i=1}^k (-1)^{k+i} a(\nu, \tau_i) \frac{r(\tau_i)}{a(\tau_i, \tau_i)} (-1)^{k-i} (-1)^{k-1} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i) \prod_{\substack{j=1 \\ j \neq i}}^k \frac{r(\tau_j)}{a(\tau_j, \tau_j)} =$$

$$(-1)^{k-1} \sum_{i=1}^k a(\nu, \tau_i) S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i) \prod_{j=1}^k \frac{r(\tau_j)}{a(\tau_j, \tau_j)}.$$

With (5.71) it then follows that the numerator of (5.61) equals

$$(-1)^k \prod_{j=1}^k \frac{r(\tau_j)}{a(\tau_j, \tau_j)} \left( r(\nu) |A(\tau_1, \dots, \tau_k)| - \sum_{i=1}^k a(\nu, \tau_i) S_{(\tau_1, \dots, \tau_k \setminus \tau_i)}(\tau_i) \right),$$

which by (5.47) is equal to  $(-1)^k S_k(\tau_1, \dots, \tau_k; \nu) \prod_{j=1}^k \frac{r(\tau_j)}{a(\tau_j, \tau_j)}$ . This result together with expressions (5.70) for the denominator and (5.51) in Lemma 5 now yield the validity of the statement for the case that all  $r(\tau_i) \neq 0$ . By applying l'Hôpital's argument the result can be extended to cases in which  $(\tau_1, \dots, \tau_k)$  is such that  $r$  has isolated zeros at on or more of the  $\tau_i, i = 1, \dots, k$ .

## 5.5.3 Proof of Lemma 9

## 5.5.3.1 Proof of Lemma 9.1

Let  $D_i(A(\tau_1, \dots, \tau_k, \tau_k))$  denote the matrix obtained by differentiating each element in the  $i$ -th column of  $A(\tau_1, \dots, \tau_{k+1})$  with respect to  $\tau_{k+1}$ , and subsequently taking  $\tau_{k+1} = \tau_k$ . Then for  $i = 1, \dots, k-1$ , the determinant  $|D_i(A(\tau_1, \dots, \tau_k, \tau_k))| = 0$ , since the  $k$ -th and  $k+1$ -th column in  $D_i(A(\tau_1, \dots, \tau_k, \tau_k))$  are equal. Therefore

$$\partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_k, \tau_k)| = |D_k(A(\tau_1, \dots, \tau_k, \tau_k))| + |D_{k+1}(A(\tau_1, \dots, \tau_k, \tau_k))|,$$

with

$$|D_k(A(\tau_1, \dots, \tau_k, \tau_k))| = \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & \cdot & \cdot & a(\tau_1, \tau_{k-1}) & 0 & a(\tau_1, \tau_k) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_{k-1}, \tau_1) & \cdot & \cdot & \cdot & a(\tau_{k-1}, \tau_{k-1}) & 0 & a(\tau_{k-1}, \tau_k) \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & 0 & a(\tau_k, \tau_k) \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & \partial_{1,0}a(\tau_k, \tau_k) & a(\tau_k, \tau_k) \end{pmatrix} \right|, \quad (5.72)$$

and

$$|D_{k+1}(A(\tau_1, \dots, \tau_k, \tau_k))| = \left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & \cdot & \cdot & a(\tau_1, \tau_{k-1}) & a(\tau_1, \tau_k) & \partial_{0,1}a(\tau_1, \tau_k) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_{k-1}, \tau_1) & \cdot & \cdot & \cdot & a(\tau_{k-1}, \tau_{k-1}) & a(\tau_{k-1}, \tau_k) & \partial_{0,1}a(\tau_{k-1}, \tau_k) \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & a(\tau_k, \tau_k) & \partial_{0,1}a(\tau_k, \tau_k) \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & a(\tau_k, \tau_k) & \partial_{1,0}a(\tau_k, \tau_k) + \partial_{0,1}a(\tau_k, \tau_k) \end{pmatrix} \right|. \quad (5.73)$$

Exchanging the two last columns in the matrix of (5.72) yields a matrix whose first  $k$  columns are equal to that in the matrix in (5.73), and whose determinant equals  $-|D_k(A(\tau_1, \dots, \tau_k, \tau_k))|$ . So  $\partial_{0, \dots, 0, 1}|A(\tau_1, \dots, \tau_k, \tau_k)|$  equals

$$\left| \begin{pmatrix} a(\tau_1, \tau_1) & \cdot & \cdot & \cdot & a(\tau_1, \tau_{k-1}) & a(\tau_1, \tau_k) & \partial_{0,1}a(\tau_1, \tau_k) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a(\tau_{k-1}, \tau_1) & \cdot & \cdot & \cdot & a(\tau_{k-1}, \tau_{k-1}) & a(\tau_{k-1}, \tau_k) & \partial_{0,1}a(\tau_{k-1}, \tau_k) \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & a(\tau_k, \tau_k) & \partial_{0,1}a(\tau_k, \tau_k) \\ a(\tau_k, \tau_1) & \cdot & \cdot & \cdot & a(\tau_k, \tau_{k-1}) & a(\tau_k, \tau_k) & \partial_{0,1}a(\tau_k, \tau_k) \end{pmatrix} \right| = 0, \quad (5.74)$$

since the last two rows in the matrix are equal.

### 5.5.3.2 Proof of Lemma 9.2

In (5.56) we replace  $k$  by  $k + 1$ , set  $l$  equal to 1 and take  $j_1 = k$ , and take  $i$  equal to  $k + 1$ . We then obtain that

$$\begin{aligned} |A(\tau_1, \dots, \tau_{k+1} \setminus \tau_k)| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - |A(\tau_1, \dots, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_{k+1} \setminus \tau_k, \tau_{k+1}; \tau_{k+1}) = \\ - |A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_k; \tau_k), \end{aligned}$$

i.e.,

$$\begin{aligned} |A(\tau_1, \dots, \tau_{k-1}, \tau_{k+1})| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - |A(\tau_1, \dots, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k+1}) = \\ - |A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k). \quad (5.75) \end{aligned}$$

Differentiating the left- and right hand side of this expression with respect to  $\tau_{k+1}$  yields

$$\begin{aligned} & \partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k-1}, \tau_{k+1})| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + |A(\tau_1, \dots, \tau_{k-1}, \tau_{k+1})| \partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - \\ & \partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k+1}) - |A(\tau_1, \dots, \tau_{k+1})| \partial_{0,\dots,0,1} S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k+1}) = \\ & - \partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k) - |A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| \partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k). \end{aligned}$$

Taking variable  $\tau_{k+1}$  equal to  $\tau_k$  makes  $S_k(\tau_1, \dots, \tau_k; \tau_{k+1})$  as well as  $S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k)$  equal to 0. Also,  $|A(\tau_1, \dots, \tau_k, \tau_{k+1})|$  and, by the first part of the Lemma,  $\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})|$  become 0. Furthermore,  $|A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}|$  becomes equal to  $|A(\tau_1, \dots, \tau_k)|$ . We obtain that  $|A(\tau_1, \dots, \tau_{k-1}, \tau_k)| \partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_k; \tau_k) = -|A(\tau_1, \dots, \tau_k)| \partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k)$ , which also follows from the fact that the function  $\tau \mapsto S_k(\tau_1, \dots, \tau_{k-1}, \tau; \tau)$  is identical to the zero function (Corollary 6, fourth statement), and therefore  $\partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) + \partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) = 0$ .

Differentiating the left- and right hand side of (5.75) twice with respect to  $\tau_{k+1}$  yields



$$\begin{aligned}
& \partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k-1}, \tau_{k+1})| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + 2 \partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k-1}, \tau_{k+1})| \partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + \\
& |A(\tau_1, \dots, \tau_{k-1}, \tau_{k+1})| \partial_{0,\dots,0,2} S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - \partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k+1}) - \\
& 2\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})| \partial_{0,\dots,0,1} S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k+1}) - |A(\tau_1, \dots, \tau_{k+1})| \partial_{0,\dots,0,2} S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k+1}) = \\
& - \partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k) - \\
& 2 \partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| \partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k) - |A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}| \partial_{0,\dots,0,2,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k).
\end{aligned}$$

Again setting  $\tau_{k+1}$  equal to  $\tau_k$  and using  $\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_k, \tau_k)| = 0$ , we get the equality

$$\begin{aligned}
& 2 \frac{d|A(\tau_1, \dots, \tau_{k-1}, \tau_k)|}{d\tau_k} \partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_k; \tau_k) + |A(\tau_1, \dots, \tau_{k-1}, \tau_k)| \partial_{0,\dots,0,2} S_k(\tau_1, \dots, \tau_k; \tau_k) - \\
& \partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_k)| S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k) = \\
& - 2 \frac{d|A(\tau_1, \dots, \tau_{k+1})_{(k,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k} \partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) - |A(\tau_1, \dots, \tau_k)| \partial_{0,\dots,0,2,0} S_k(\tau_1, \dots, \tau_k; \tau_k).
\end{aligned}$$

Since  $|A(\tau_1, \dots, \tau_k)| \neq 0$  (because  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$ ) we may write (see (5.49))  $\hat{x}_k(\tau_1, \dots, \tau_k) = -\frac{S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k)}{|A(\tau_1, \dots, \tau_k)|}$ . The previous expression then can be rewritten as

$$-\frac{2}{|A(\tau_1, \dots, \tau_k)|} \times \left( \frac{d|A(\tau_1, \dots, \tau_{k+1})|_{(k,k+1)}}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k} \partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) + \frac{d|A(\tau_1, \dots, \tau_{k-1}, \tau_k)|}{d\tau_k} \partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_k; \tau_k) \right) - \partial_{0,\dots,0,2} |A(\tau_1, \dots, \tau_k, \tau_k)| \hat{x}_k(\tau_1, \dots, \tau_k) = \partial_{0,\dots,0,2,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) + \partial_{0,\dots,0,2} S_k(\tau_1, \dots, \tau_k; \tau_k). \quad (5.76)$$

Since (see (5.51))  $S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) = |A(\tau_1, \dots, \tau_k)| s_k(\tau_1, \dots, \tau_k; \tau_{k+1})$ , and the function  $\tau \mapsto S_k(\tau, \dots, \tau_{k-1}, \tau; \tau)$  equals the zero function, it follows, since  $\langle \tau_1, \dots, \tau_k \rangle$  belongs to the  $k$ -isocline, i.e.,  $\partial_{0,\dots,0,1} s_k(\tau_1, \dots, \tau_k; \tau_k) = 0$ , that both  $\partial_{0,\dots,0,1} S_k(\tau_1, \dots, \tau_k; \tau_k) = 0$  and  $\partial_{0,\dots,0,1,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) = 0$  hold. Furthermore, because by the first part of this Lemma  $\partial_{0,\dots,0,1} |A(\tau_1, \dots, \tau_k, \tau_k)| = 0$ , the equality  $\partial_{0,\dots,0,2,0} S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) = |A(\tau_1, \dots, \tau_k)| \partial_{0,\dots,0,2,0} s_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k)$  holds. Finally,  $\partial_{0,\dots,0,2} S_k(\tau_1, \dots, \tau_k; \tau_k) = |A(\tau_1, \dots, \tau_k)| \partial_{0,\dots,0,2} s_k(\tau_1, \dots, \tau_k; \tau_k)$ . Equality (5.76) then becomes

$$-\partial_{0,\dots,0,2} |A(\tau_1, \dots, \tau_k, \tau_k)| \hat{x}_k(\tau_1, \dots, \tau_k) = |A(\tau_1, \dots, \tau_k)| (\partial_{0,\dots,0,2,0} s_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) + \partial_{0,\dots,0,2} s_k(\tau_1, \dots, \tau_k; \tau_k)) \quad (5.77)$$

Since by assumption both  $\hat{x}_k(\tau_1, \dots, \tau_k) > 0$  and  $\partial_{0,\dots,0,2,0} s_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) + \partial_{0,\dots,0,2} s_k(\tau_1, \dots, \tau_k; \tau_k) > 0$ , it follows for values  $\tau_{k+1}$  sufficiently close to  $\tau_k$  that  $\text{sign}(|A(\tau_1, \dots, \tau_k, \tau_{k+1})|) = -\text{sign}(|A(\tau_1, \dots, \tau_k)|)$ .

#### 5.5.4 Proof of Lemma 10

The validity of the Lemma is derived by means of induction. We first prove that for  $k = 2$  the equality  $\partial_{0,1,0}S_2(\tau_1, \tau_1, \nu) = 0$  holds. By (5.47) we have that  $S_2(\tau_1, \tau_2; \nu) = r(\nu)|A(\tau_1, \tau_2)| - a(\nu, \tau_1)S_1(\tau_2; \tau_1) - a(\nu, \tau_2)S_1(\tau_1; \tau_2)$ . Differentiating with respect to  $\tau_2$  yields that

$$\partial_{0,1,0}S_2(\tau_1, \tau_2; \nu) = r(\nu)\partial_{0,1}|A(\tau_1, \tau_2)| - a(\nu, \tau_1)\partial_{1,0}S_1(\tau_2; \tau_1) - \partial_{0,1}a(\nu, \tau_2)S_1(\tau_1; \tau_2) - a(\nu, \tau_2)\partial_{0,1}S_1(\tau_1; \tau_2).$$

By taking  $\tau_2$  equal to  $\tau_1$ , and using that  $\partial_{0,1}|A(\tau_1, \tau_1)| = 0$  (Lemma 9.1) and  $S_1(\tau_1; \tau_1) = 0$  we obtain that  $\partial_{0,1,0}S_2(\tau_1, \tau_1; \nu) = -a(\nu, \tau_1)(\partial_{1,0}S_1(\tau_1; \tau_1) + \partial_{0,1}S_1(\tau_1; \tau_1)) = 0$ , since the function  $\tau \mapsto S_1(\tau; \tau)$  is equal to the zero function.

The induction hypothesis states that  $\partial_{0,\dots,0,1,0}S_{k-1}(\tau_1, \dots, \tau_{k-2}, \tau_{k-2}; \nu) = 0$ . Writing (again by (5.47))  $S_k(\tau_1, \dots, \tau_k; \nu) = r(\nu)|A(\tau_1, \dots, \tau_k)| - \sum_{i=1}^k a(\nu, \tau_i)S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)$  and differentiating with respect to  $\tau_k$  we get that

$$\partial_{0,\dots,0,1,0}S_k(\tau_1, \dots, \tau_k; \nu) =$$

$$r(\nu)\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_k)| - \sum_{i=1}^{k-2} a(\nu, \tau_i)\partial_{0,\dots,0,1,0}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i) - a(\nu, \tau_{k-1})\partial_{0,\dots,0,1,0}S_{k-1}(\tau_1, \dots, \tau_{k-2}, \tau_k; \tau_{k-1}) -$$

$$\partial_{0,1}a(\nu, \tau_k)S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k) - a(\nu, \tau_k)\partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k). \quad (5.78)$$

Taking  $\tau_k = \tau_{k-1}$  sets  $\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k-1}, \tau_k)|$  equal to 0 (Lemma 9.1), as well as  $\partial_{0,\dots,0,1,0}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_i; \tau_i)$  for  $i = 1, \dots, k-2$  (induction hypothesis) and  $S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_k)$ . The remaining part in the right hand side of (5.78) becomes

$-a(\nu, \tau_{k-1})(\partial_{0,\dots,0,1,0} S_{k-1}(\tau_1, \dots, \tau_{k-2}, \tau_{k-1}; \tau_{k-1}) + \partial_{0,\dots,0,1} S_{k-1}(\tau_1, \dots, \tau_{k-1}; \tau_{k-1}))$ , which again equals 0 since  $\tau \mapsto S_{k-1}(\tau_1, \dots, \tau_{k-2}, \tau; \tau)$  is identical to the zero function.

5.5.5 Proof of Lemma 11

5.5.5.1 Proof of Lemma 11.1

In (5.57) we take  $l = 1$ , and  $j_1 = j \in \{1, \dots, k\}$  and obtain the equality

$$|A(\tau_1, \dots, \tau_k \setminus \tau_j)| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - |A(\tau_1, \dots, \tau_k)| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) = (-1)^{j-(k+1)} |A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_j). \quad (5.79)$$

Differentiating with respect to  $\tau_{k+1}$  we get that

$$|A(\tau_1, \dots, \tau_k \setminus \tau_j)| \partial_{0, \dots, 0, 1} S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - |A(\tau_1, \dots, \tau_k)| \partial_{0, \dots, 0, 1} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) = (-1)^{j-(k+1)} \partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_j). \quad (5.80)$$

Setting  $\tau_{k+1} = \tau_k$ , and using the fact that  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  belongs to the  $k$ -isocline yields that

$$- |A(\tau_1, \dots, \tau_k)| \partial_{0, \dots, 0, 1} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k) = (-1)^{j-(k+1)} \frac{d|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_j), \quad (5.81)$$

i.e.,

$$\partial_{0, \dots, 0, 1} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k) = (-1)^{j-(k+1)} \frac{d|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k} \hat{x}_j(\tau_1, \dots, \tau_k). \quad (5.82)$$

Since  $\hat{x}_j(\tau_1, \dots, \tau_k) > 0$ , it follows that

$$\text{sign}(\partial_{0, \dots, 0, 1} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k)) = - \text{sign} \left( (-1)^{j-k} \frac{d|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k} \right). \quad (5.83)$$

## 5.5.5.2 Proof of Lemma 11.2

In (5.56) we replace  $k$  by  $k + 1$ , take  $l = 1$  and  $j_1 = j \in \{1, \dots, k - 1\}$ , and  $i = k + 1$ . We obtain the equality

$$\begin{aligned} |A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - |A(\tau_1, \dots, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) = \\ (-1)^{j-(k+1)} |A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j). \end{aligned} \quad (5.84)$$

Differentiating with respect to  $\tau_{k+1}$  yields that

$$\begin{aligned} \partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + |A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| \partial_{0, \dots, 0, 1} S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - \\ \partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_k, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) - |A(\tau_1, \dots, \tau_{k+1})| \partial_{0, \dots, 0, 1} S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) = \\ (-1)^{j-(k+1)} \partial_{0, \dots, 0, 1} |A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) + \\ (-1)^{j-(k+1)} |A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| \partial_{0, \dots, 0, 1, 0} S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j). \end{aligned} \quad (5.85)$$

Taking  $\tau_{k+1} = \tau_k$  in this expression yields  $0 = 0$ . Differentiating twice with respect to  $\tau_{k+1}$  in (5.84) renders the equality

$$\begin{aligned}
& \partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + 2\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| \partial_{0,\dots,0,1}S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + \\
& |A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| \partial_{0,\dots,0,2}S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - \partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) - \\
& 2\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_k, \tau_{k+1})| \partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) - |A(\tau_1, \dots, \tau_k, \tau_{k+1})| \partial_{0,\dots,0,2}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) = \\
& (-1)^{j-(k+1)}\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) + \\
& (-1)^{j-(k+1)} 2\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| \partial_{0,\dots,0,1,0}S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) + \\
& (-1)^{j-(k+1)}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| \partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j). \quad (5.86)
\end{aligned}$$

Taking  $\tau_{k+1}$  equal to  $\tau_k$ , and making use of Corollary 6.5, Lemmas 9.1 and 10 yields again  $0 = 0$ . We differentiate once more with respect to  $\tau_{k+1}$ , and obtain

$$\begin{aligned}
& \partial_{0,\dots,0,3}|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + 3\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| \partial_{0,\dots,0,1}S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + \\
& \quad 3\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| \partial_{0,\dots,0,2}S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) + |A(\tau_1, \dots, \tau_{k+1} \setminus \tau_j)| \partial_{0,\dots,0,3}S_k(\tau_1, \dots, \tau_k; \tau_{k+1}) - \\
& \quad \partial_{0,\dots,0,3}|A(\tau_1, \dots, \tau_k, \tau_{k+1})| S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) - 3\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_{k+1})| \partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) - \\
& \quad 3\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_k, \tau_{k+1})| \partial_{0,\dots,0,2}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) - |A(\tau_1, \dots, \tau_k, \tau_{k+1})| \partial_{0,\dots,0,3}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_{k+1}) = \\
& (-1)^{j-(k+1)}\partial_{0,\dots,0,3}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) + \\
& \quad (-1)^{j-(k+1)} 3\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| \partial_{0,\dots,0,1,0}S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) + \\
& \quad (-1)^{j-(k+1)} 3\partial_{0,\dots,0,1}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| \partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j) + \\
& \quad (-1)^{j-(k+1)}|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}| \partial_{0,\dots,0,3,0}S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j). \quad (5.87)
\end{aligned}$$



We again take  $\tau_{k+1} = \tau_k$ . Using the fact that  $\langle \tau_1, \dots, \tau_k \rangle \in \mathbb{A}_k$  belongs to the  $k$ -isocline, as well as Corollary 6.5 and Lemmas 9.1 and 10, reduces the previous equality to

$$\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_k)| \partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k) = (-1)^{j-k} \frac{d|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k} \partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_j). \quad (5.88)$$

In the first part of the Lemma we derived that

$\text{sign}(\partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k)) = -\text{sign}\left((-1)^{j-k} \frac{d|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k}\right)$ . Since by assumption  $\partial_{0,\dots,0,2}S_k(\tau_1, \dots, \tau_k; \tau_k) + \partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_{k-1}, \tau_k; \tau_k) > 0$ , we know from Lemma 9.2 and its proof that  $\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_k)| \neq 0$  (see (5.77)). We conclude from (5.88) that

$$\frac{\partial_{0,\dots,0,2,0}S_k(\tau_1, \dots, \tau_k, \tau_k \setminus \tau_j; \tau_j)}{\partial_{0,\dots,0,2}|A(\tau_1, \dots, \tau_k, \tau_k)|} = (-1)^{j-k} \frac{\partial_{0,\dots,0,1}S_{k-1}(\tau_1, \dots, \tau_k \setminus \tau_j; \tau_k)}{\frac{d|A(\tau_1, \dots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}} \Big|_{\tau_{k+1}=\tau_k}} < 0. \quad (5.89)$$

## 5.5.6 Proof of Lemma 12

Firstly, given that  $LV_k(\tau_1, \dots, \tau_k)$  is fully subregular, the fact that  $LV_k(\tau'_1, \dots, \tau'_k)$  is fully subregular for  $(\tau'_1, \dots, \tau'_k)$  sufficiently close to  $(\tau_1, \dots, \tau_k)$  follows immediately from the continuity of the function  $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \mapsto |A(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})|$ , for any  $l = 1, \dots, k$  and any set  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ .

It remains to be shown that  $s$ -permanence of  $LV_k(\tau_1, \dots, \tau_k)$  is maintained under sufficiently small changes of  $(\tau_1, \dots, \tau_k)$  into  $(\tau'_1, \dots, \tau'_k)$ . Let  $p_1, \dots, p_k$  be positive numbers such that for each  $l = 1, \dots, k$  and each subset  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  (with mutually distinct  $i_1, \dots, i_l$ ) for which

$\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists, the condition

$$\sum_{\alpha=1}^l p_{i_\alpha} s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{i_\alpha}) > 0 \quad (5.90)$$

holds. We seek positive numbers  $p'_1, \dots, p'_k$  such that for each  $l = 1, \dots, k$  and each subset  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  (with  $i_1, \dots, i_l$  again mutually distinct) for which  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists,

$$\sum_{\beta=1}^l p'_{j_\beta} s_{k-l}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}; \tau'_{j_\beta}) > 0. \quad (5.91)$$

We consider the generic and the non-generic case.

Case I (The generic case.) For each  $l = 1, \dots, k$  and each  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ ,  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists if and only if  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists. The change from  $(\tau_1, \dots, \tau_k)$  into  $(\tau'_1, \dots, \tau'_k)$  then causes a change in the equilibrium values, but does not cause the appearance of additional equilibria. The positivity of the numbers  $p_1, \dots, p_k$ , the continuity of the functions  $(\tau_1, \dots, \tau_k) \mapsto s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{i_\alpha})$ ,  $\alpha \in \{1, \dots, l\}$ , and the positivity of the summation in (5.90) then imply that there is an open neighbourhood  $U$  of  $(\tau_1, \dots, \tau_k)$  in  $\mathbb{T}^k$ , and an open neighbourhood  $V$  of  $(p_1, \dots, p_k)$  in  $\text{int}(\mathbb{R}_+^k)$ , such that for any  $(\tau'_1, \dots, \tau'_k) \in U$  and any  $(p'_1, \dots, p'_k) \in V$  expression (5.91) is satisfied for each  $l = 1, \dots, k$  and each subset  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  for which  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists.

Case II (The non-generic case.) Let  $I$  denote the collection of sets  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  (for any  $l = 1, \dots, k$ ) for which  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists. Under sufficiently small changes of  $(\tau_1, \dots, \tau_k)$  into  $(\tau'_1, \dots, \tau'_k)$ , then also the equilibrium  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists. In the non-generic case in addition there is a sub-collection  $J$  of these sets  $\{i_1, \dots, i_l\}$  such that for each element in  $J$  there exists at least one non-empty subset  $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\}$ , with  $l' < l$ , for which the equilibrium  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{j_1}, \dots, \tau'_{j_{l'}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k))$  comes into existence due to the change from  $(\tau_1, \dots, \tau_k)$  into  $(\tau'_1, \dots, \tau'_k)$  (which implies that  $\{j_1, \dots, j_{l'}\}$  itself does not belong to  $I$ ). For a given  $\{i_1, \dots, i_l\} \in J$  and  $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\}$  this happens if due to this change a bifurcation occurs in which  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  splits into two equilibria:  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  and  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{j_1}, \dots, \tau'_{j_{l'}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k))$ . For  $LV_k(\tau_1, \dots, \tau_k)$  it then is required that, with  $\alpha \in \{1, \dots, k\} \setminus \{i_1, \dots, i_l\}$  and  $\beta \in \{i_1, \dots, i_l\} \setminus \{j_1, \dots, j_{l'}\}$ , the restriction to  $\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k)$  of the isoclines  $r(\tau_\alpha) + \sum_{j=1}^k a(\tau_\alpha, \tau_j)x_j = 0$  and  $r(\tau_\beta) + \sum_{j=1}^k a(\tau_\beta, \tau_j)x_j = 0$  (i.e.,  $r(\tau_\alpha) + \sum_{\substack{j=1 \\ j \notin \{j_1, \dots, j_{l'}\}}}^k a(\tau_\alpha, \tau_j)x_j = 0$  and  $r(\tau_\beta) + \sum_{\substack{j=1 \\ j \notin \{j_1, \dots, j_{l'}\}}}^k a(\tau_\beta, \tau_j)x_j = 0$ ) intersect in  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ . Consequently,

$$s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_\beta) = 0 \text{ for } \beta \in \{i_1, \dots, i_l\} \setminus \{j_1, \dots, j_{l'}\}. \quad (5.92)$$

In the community state space of  $LV_k(\tau'_1, \dots, \tau'_k)$  the equilibrium  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  then is the intersection of the restriction to  $\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k)$  of the isoclines  $r(\tau'_\alpha) + \sum_{j=1}^k a(\tau'_\alpha, \tau'_j)x_j = 0$ ,  $\alpha \in \{1, \dots, k\} \setminus \{i_1, \dots, i_l\}$ , with  $\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k)$ . The equilibrium  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{j_1}, \dots, \tau'_{j_{l'}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k))$  is the intersection of the isoclines  $r(\tau'_\alpha) + \sum_{j=1}^k a(\tau'_\alpha, \tau'_j)x_j = 0$ ,  $\alpha \in \{1, \dots, k\} \setminus \{i_1, \dots, i_l\}$ , with the isoclines

$r(\tau'_\beta) + \sum_{j=1}^k a(\tau'_\beta, \tau'_j)x_j$ ,  $\beta \in \{i_1, \dots, i_l\} \setminus \{j_1, \dots, j_{l'}\}$ , with both collections of isoclines restricted to  $\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k)$ .

As in the generic case, it follows that there exist a neighbourhood  $U_1$  of  $(\tau'_1, \dots, \tau'_k)$  in  $\mathbb{T}^k$  and a neighbourhood  $V_1$  of  $(p'_1, \dots, p'_k)$  in  $\text{int}(\mathbb{R}_+^k)$  such that (5.91) is satisfied for all  $(\tau'_1, \dots, \tau'_k) \in U_1$  and all  $(p'_1, \dots, p'_k) \in V_1$ , for all equilibria  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ , for all  $l = 1, \dots, k$  and all  $\{i_1, \dots, i_l\} \in I \setminus J$ .

Next, let  $\{i_1, \dots, i_l\} \in J$ , and  $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\}$ , such that under the change from  $(\tau_1, \dots, \tau_k)$  into  $(\tau'_1, \dots, \tau'_k)$  the equilibrium  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  splits into  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  and  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{j_1}, \dots, \tau'_{j_{l'}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k))$ . For any such set  $\{i_1, \dots, i_l\} \in J$  expression (5.90) due to (5.92) can be rewritten as

$$\sum_{\substack{\alpha=1 \\ i_\alpha \in \{j_1, \dots, j_{l'}\}}}^l p_{i_\alpha} s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{i_\alpha}) > 0. \quad (5.93)$$

For  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l})$  it follows (for any numbers  $p'_1, \dots, p'_k$ ) that

$$\begin{aligned} \sum_{\alpha=1}^l p'_{i_\alpha} s_{k-l}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}; \tau'_{i_\alpha}) = \\ \sum_{\substack{\alpha=1 \\ i_\alpha \in \{j_1, \dots, j_{l'}\}}}^l p'_{i_\alpha} s_{k-l}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}; \tau'_{i_\alpha}) + \\ \sum_{\substack{\alpha=1 \\ i_\alpha \in \{i_1, \dots, i_l\} \setminus \{j_1, \dots, j_{l'}\}}}^l p'_{i_\alpha} s_{k-l}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}; \tau'_{i_\alpha}). \end{aligned} \quad (5.94)$$

From (5.93) it follows for  $(\tau'_1, \dots, \tau'_k)$  sufficiently close to  $(\tau_1, \dots, \tau_k)$  and  $(p'_1, \dots, p'_k)$  sufficiently close to  $(p_1, \dots, p_k)$ , that the first summation in the right hand side of this expression is positive, for any  $\{i_1, \dots, i_l\} \in J$ . From (5.92) it follows that for  $(\tau'_1, \dots, \tau'_k)$  sufficiently close to  $(\tau_1, \dots, \tau_k)$  and  $(p'_1, \dots, p'_k)$  sufficiently close to  $(p_1, \dots, p_k)$ , the second summation in (5.94) can be taken to be arbitrarily small, for any  $\{i_1, \dots, i_l\} \in J$ . Therefore, there exist an open neighbourhood  $U_2$  of  $(\tau'_1, \dots, \tau'_k)$  in  $\mathbb{T}^k$  and an open neighbourhood  $V_2$  of  $(p_1, \dots, p_k)$  in  $\text{int}(\mathbb{R}_+^k)$  such that (5.91) is satisfied for

all  $(\tau'_1, \dots, \tau'_k) \in U_2$  and all  $(p'_1, \dots, p'_k) \in V_2$ , for all equilibria  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{i_1}, \dots, \tau'_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$ , for all  $l = 1, \dots, k$  and all  $\{i_1, \dots, i_l\} \in J$ .

For  $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\} \in J$  we notice, by Lemma 4 and expression (5.92), that  $s_{k-l'}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l'}}; \tau_{j_\beta})$  equals  $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{j_\beta})$ ,  $\beta = 1, \dots, l'$ . Therefore, with (5.93),

$$\begin{aligned} \sum_{\beta=1}^{l'} p_\beta s_{k-l'}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l'}}; \tau_{j_\beta}) &= \\ \sum_{\beta=1}^{l'} p_\beta s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{j_\beta}) &> 0. \end{aligned} \quad (5.95)$$

It follows that there exist an open neighbourhood  $U_3$  of  $(\tau_1, \dots, \tau_k)$  in  $\mathbb{T}^k$  and an open neighbourhood  $V_3$  of  $(p_1, \dots, p_k)$  in  $\text{int}(\mathbb{R}_+^k)$  such that (5.91) is satisfied for all  $(\tau'_1, \dots, \tau'_k) \in U_3$  and all  $(p'_1, \dots, p'_k) \in V_3$ , for all possible equilibria  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau'_{j_1}, \dots, \tau'_{j_{l'}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l'}}(\mathbb{R}_+^k))$ , for all  $l = 1, \dots, k$  and all  $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\} \in J$ .

By taking  $(\tau'_1, \dots, \tau'_k) \in U_1 \cap U_2 \cap U_3$  and  $(p'_1, \dots, p'_k) \in V_1 \cap V_2 \cap V_3$  it follows that (5.91) holds for any  $l = 1, \dots, k$  and any  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  for which the equilibrium  $\hat{x}(\tau'_1, \dots, \tau'_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists. This proves the non-generic case.

## 5.5.7 Proof of Lemma 13

Without loss of generality we may assume that  $i$  equals  $k$ , and we shall do so here.

The  $s$ -permanence of  $LV_k(\tau_1, \dots, \tau_k)$  implies the existence of  $k$  strictly positive numbers  $p_1, \dots, p_k$  such that for each  $l$  and each subset  $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$  such that  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \text{int}(\text{bd}_{i_1, \dots, i_l}(\mathbb{R}_+^k))$  exists,

$$\sum_{\alpha=1}^l p_{i_\alpha} s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{i_\alpha}) > 0. \quad (5.96)$$

We seek  $k+1$  strictly positive numbers  $p'_1, \dots, p'_{k+1}$  such that for each  $l = 1, \dots, k+1$  and each subset  $\{j_1, \dots, j_l\} \subset \{1, \dots, k+1\}$  (of mutually distinct elements) for which  $\hat{x}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in \text{int}(\text{bd}_{j_1, \dots, j_l}(\mathbb{R}_+^{k+1}))$  exists, the summation

$$\sum_{\beta=1}^l p'_{j_\beta} s_{k+1-l}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{j_\beta}). \quad (5.97)$$

is positive.

We first restrict ourselves to the case  $l = 1$ . For each  $j \in \{1, \dots, k+1\}$  such that  $\hat{x}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_j) \in \text{int}(\text{bd}_j(\mathbb{R}_+^{k+1}))$  exists,  $p'_j s_k(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j) > 0$  then is required to hold. I.e., both

$$p'_k s_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k) > 0, \quad (5.98)$$

and

$$p'_{k+1} s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) > 0 \quad (5.99)$$

must hold, and in addition for each  $j = 1, \dots, k-1$

$$p'_j s_k(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j) > 0 \quad (5.100)$$

must hold. Since both  $s_k(\tau_1, \dots, \tau_{k-1}, \tau_{k+1}; \tau_k) > 0$  and  $s_k(\tau_1, \dots, \tau_k; \tau_{k+1}) > 0$  for  $\tau_{k+1}$  sufficiently close (but not equal) to  $\tau_k$ , it follows that in case  $l = 1$ ,  $p'_k$  and  $p'_{k+1}$  can taken to be arbitrarily positive numbers. For  $j = 1, \dots, k-1$ , we obtain from (5.66) that for  $\tau_{k+1}$  sufficiently close (but not equal) to  $\tau_k$  that  $\hat{x}_j(\tau_1, \dots, \tau_{k+1}) > 0$ . With (5.49) and Lemma 9.2 it then follows for such  $\tau_{k+1}$  that  $s_k(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j) > 0$ . This then implies that for  $l = 1$  also the  $p'_j$ ,  $j = 1, \dots, k-1$ , in (5.100) can taken to be arbitrarily positive numbers. We conclude that there is an open neighbourhood  $U_1$  of  $\tau_k$  in  $\mathbb{R}$  such that for each  $\tau_{k+1} \neq \tau_k$  in  $U_1$ , expression (5.97) is positive for  $l = 1$  and each  $j \in \{1, \dots, k+1\}$  such that  $\hat{x}(\tau_1, \dots, \tau_{k+1} \setminus \tau_j) \in \text{int}(\text{bd}_j(\mathbb{R}_+^{k+1}))$  exists, for arbitrarily positive  $p'_1, \dots, p'_{k+1}$

We now consider  $l = 2, \dots, k+1$ . We distinguish four mutually exclusive cases for the summations (5.97), that together cover all possible summations as determined by the sets  $\{j_1, \dots, j_l\} \subset \{1, \dots, k+1\}$ ,  $l = 2, \dots, k+1$ . We assume the  $j_\beta$ ,  $\beta = 1, \dots, l$  to satisfy  $j_1 < \dots < j_l$ .

1.  $j_{l-1} = k, j_l = k+1$ . The summation (5.97) then becomes

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + p'_{k+1} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{k+1}) =$$

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + p'_{k+1} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_k) +$$

$$\epsilon p'_{k+1} \partial_{0, \dots, 0, 1} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_k) + o(\epsilon^2) \quad (\epsilon \rightarrow 0). \quad (5.101)$$

By taking  $p'_{j_\beta}$  to be equal to  $p_{j_\beta}$ , for  $\beta = 1, \dots, l-1$ , the first summation in the last expression by assumption becomes positive, for each choice of  $l \in \{2, \dots, k+1\}$  and each  $\{j_1, \dots, j_{l-2}\} \subset \{1, \dots, k-1\}$  such that  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l-1}}(\mathbb{R}_+^k))$  exists. By taking  $p'_{k+1}$  positive and such that

$$p'_{k+1} < \min_{\substack{l=2, \dots, k+1 \\ \{j_1, \dots, j_{l-2}\} \subset \{1, \dots, k-1\} \\ \hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l-1}}(\mathbb{R}_+^k))}} \frac{\sum_{\beta=1}^{l-1} p_{j_\beta} s_{k-(l+1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta})}{|s_{k-(l+1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_k)|}, \quad (5.102)$$

it follows that for  $\tau_{k+1} \neq \tau_k$  sufficiently close to  $\tau_k$ , expression (5.97) then is positive. I.e., there is an open neighbourhood  $U_2$  of  $\tau_k$  in  $\mathbb{R}$  such that for each  $\tau_{k+1} \neq \tau_k$  that belongs to  $U_2$ , expression (5.97) is positive for  $l = 2, \dots, k+1$  and  $\{j_1, \dots, j_l\} \subset \{1, \dots, k+1\}$ , with  $j_l = k$ ,  $j_{l+1} = k+1$ , and such that  $\hat{x}(\tau_1, \dots, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in \text{int}(\text{bd}_{j_1, \dots, j_l}(\mathbb{R}_+^{k+1}))$  exists.

2.  $k \notin \{j_1, \dots, j_{l-1}\}$ ,  $j_l = k+1$ . We then obtain that (5.97) equals

$$\begin{aligned} & \sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + p'_{k+1} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{k+1}) = \\ & \sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + \epsilon p'_{k+1} \partial_{0, \dots, 0, 1} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_k) + o(\epsilon^2) \quad (\epsilon \rightarrow 0). \end{aligned} \quad (5.103)$$

The first summation in the right hand side by assumption becomes positive by replacing  $p'_{j_\beta}$  with  $p_{j_\beta}$ ,  $\beta = 1, \dots, l-1$ , for each  $l = 2, \dots, k+1$  and each  $\{j_1, \dots, j_{l-1}\} \subset \{1, \dots, k\}$  such that  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l-1}}(\mathbb{R}_+^k))$



exists. Consequently, there is an open neighbourhood  $U_3$  of  $\tau_k$  in  $\mathbb{R}$  such that for each  $\tau_{k+1} \neq \tau_k$  that belongs to  $U_3$ , expression (5.97) is positive for  $l = 2, \dots, k+1$  and  $\{j_1, \dots, j_l\} \subset \{1, \dots, k+1\}$ , with  $k \notin \{j_1, \dots, j_{l-1}\}$  and  $j_l = k+1$ , and such that  $\hat{x}(\tau_1, \dots, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in \text{int}(\text{bd}_{j_1, \dots, j_l}(\mathbb{R}_+^{k+1}))$  exists.

3.  $j_l = k$  (and, consequently,  $k+1 \notin \{j_1, \dots, j_l\}$ ). The summation in (5.97) then yields

$$\begin{aligned} & \sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \dots, \tau_{k-1}, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + p'_k s_{k-(l-1)}(\tau_1, \dots, \tau_{k-1}, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_k) = \\ & \sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \dots, \tau_{k-1}, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + \epsilon \sum_{\beta=1}^{l-1} p'_{j_\beta} \partial_{0, \dots, 0, 1, 0} s_{k-(l-1)}(\tau_1, \dots, \tau_{k-1}, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_{j_\beta}) + \\ & \epsilon p'_k \partial_{0, \dots, 0, 1, 0} s_{k-(l-1)}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}; \tau_k) + o(\epsilon^2) \quad (\epsilon \rightarrow 0). \quad (5.104) \end{aligned}$$

In the right hand side of (5.104), the first summation by assumption becomes positive by replacing  $p'_{j_\beta}$  by  $p_{j_\beta}$ ,  $\beta = 1, \dots, l-1$ , for each  $l = 2, \dots, k+1$  and each  $\{j_1, \dots, j_{l-1}\} \subset \{1, \dots, k-1\}$  such that  $\hat{x}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l-1}}) \in \text{int}(\text{bd}_{j_1, \dots, j_{l-1}}(\mathbb{R}_+^k))$  exists. It follows that here is a neighbourhood  $U_4$  of  $\tau_k$  in  $\mathbb{R}$  such that for each  $\tau_{k+1} \neq \tau_k$  that belongs to  $U_4$  expression (5.97) is positive for each  $l = 2, \dots, k+1$  and  $\{j_1, \dots, j_l\} \subset \{1, \dots, k\}$ , with  $j_l = k$ , and such that  $\hat{x}(\tau_1, \dots, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in \text{int}(\text{bd}_{j_1, \dots, j_l}(\mathbb{R}_+^{k+1}))$  exists.

4. Both  $k \notin \{j_1, \dots, j_l\}$  and  $k+1 \notin \{j_1, \dots, j_l\}$ . This case does not have to be taken into account, since generically  $\hat{x}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \notin \text{int}(\text{bd}_{j_1, \dots, j_l}(\mathbb{R}_+^{k+1}))$ . This can be seen from expression (5.49). By this expression

$$\hat{x}_{\tau_k}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) = -\frac{S_{k-l}(\tau_1, \dots, \tau_{k-1}, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_k)}{|A(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l})|}, \text{ and}$$

$\hat{x}_{\tau_{k+1}}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) = -\frac{S_{k-l}(\tau_1, \dots, \tau_{k-1}, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_l}; \tau_{k+1})}{|A(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l})|}$ . It follows that for  $\tau_k$  and  $\tau_{k+1}$  sufficiently close to each other, the values  $\hat{x}_{\tau_k}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l})$  and  $\hat{x}_{\tau_{k+1}}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l})$  have opposite signs, and therefore  $\hat{x}(\tau_1, \dots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \notin \text{int}(\text{bd}_{j_1, \dots, j_l}(\mathbb{R}_+^{k+1}))$ .

We conclude that if  $\tau_{k+1} \in U_1 \cap U_2 \cap U_3 \cap U_4$  and not equal to  $\tau_k$ , (5.97) is positive for all  $l = 1, \dots, k$  and all  $\{j_1, \dots, j_l\} \subset \{1, \dots, k\}$  such that  $\hat{x}(\tau_1, \dots, \tau_{k+1} \setminus \tau_{j_1}, \dots, \tau_{j_l}) \in \text{bd}(\mathbb{R}_+^{k+1})$ , with the  $p'_j$  equal to  $p_j > 0$ ,  $j = 1, \dots, k$ , and with  $p'_{k+1} > 0$  satisfying expression (5.102). Therefore  $LV_{k+1}(\tau_1, \dots, \tau_{k+1})$  then is  $s$ -permanent.

# **Part III**

## **Discussion**



## DISCUSSION

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### 6.1 OPINION DYNAMICS

In the first chapter on opinion dynamics we have studied the role of inflexibles and floaters on the support for two opinions under repeated application of the local majority rule in groups of size 3. In the second chapter on opinion dynamics we refined this study by allowing for contrarian and non-contrarian floaters. We derived several scenarios for the development of opinion support in time. We shall now point to topics for further research in opinion dynamics. All these directions for research in opinion dynamics deal with adding more structure to opinion-dynamical models.

A first and straightforward way to add more realism to opinion-dynamical models is by allowing groups of varying sizes in which individuals encounter other opinions. This can be done by means of probability distributions on group sizes. Also an increase in the number of opinions will be useful in connecting with real opinion-dynamical processes.

More realism can also be achieved by by incorporation social structures. These can be of a spatial, economic and/or educational kind. Spatial structure enables to study the spreading of opinions in both rural and urban areas. In addition it allows to model a possibly higher abundance of opinions in urban areas compared to rural areas. Adding economic structure takes into account that support of opinion may depend on income, whereas educational structure deals with the support of opinion in relation to educational level. A further realistic extension of opinion models is to incorporate the role of media in the spreading of opinions, as a global influence on opinion bearers in contrast to the local influences which individuals encounter in the groups they repeatedly form.

Apart from inflexibles and (contrarian and non-contrarian) floaters it may be useful to include a class of neutrals composed of individuals who do not yet have an opinion, but may develop one by repeated encounters with opinion bearers. A further extension is the incorporation of a delay effect for floaters, which expresses that a floater builds up the inclination to change its opinion to that of the majority instead of making this change at first encounter with a majority. Another extension of opinion dynamics models is to allow for the change of inflexible into floater or vice versa. E.g., contrarian behaviour may express the adolescent attitude to strive for individualisation, which may transform into inflexible behaviour when one grows older. Fuzzy set theory can be applied to express doubt in supporting an opinion.

Political parties in general represent a number of political opinions, and part of these opinions may be characteristic for several political parties. It may therefore be insightful to model the dynamics of support for vectors of opinions instead of single opinions. An individual then is characterised by the vector of opinions he or she supports, and the opinions for which the individual is an inflexible determines the political party that one associates with. For the opinions for which an individual is not an inflexible, non-contrarian or contrarian behaviour can be assumed.

With chapters on opinion dynamics as well as adaptive dynamics in one thesis it is tempting to reflect on mutual applications. One immediate notion that comes to mind is to model with adaptive-dynamical means a phenomenon that is well-known in Dutch politics: the raise and development of a new alternative opinion or political splinterparty, and to determine under which conditions such an opinion or party becomes part of the establishment, remains present in a marginal way or disappears altogether.

## 6.2 ADAPTIVE DYNAMICS

Many works has already been done and published on the theory and applications of adaptive dynamics (see the site [60] for an overview). However, an extensive study of adaptive dynamics based on Lotka-Volterra community dynamics had not yet been performed, and Chapter 5 on adaptive dynamics in this thesis provides an opening in this direction. As is shown in this chapter, the approach allows for an explicit expression for the invasion fitness function, which turned out to be useful in stating various conclusions of adaptive dynamics. We mention several open problems of adaptive dynamics that follow from this chapter.

A main problem is the determination of the zero sets of the invasion fitness functions  $s_k(\tau_1, \dots, \tau_k; \nu)$  for arbitrary  $k \geq 1$ . The intersections of these zero sets with the diagonal hyperplanes  $\Delta_{i,k+1}^{k+1}$  determine the position and shape of the isoclines. Also, these zero sets determine the local shapes of the sets  $\mathbb{A}_{k+1}$  attached to the isoclines, and thus the shape of the space into which an evolutionary trajectory proceeds in an evolutionary branching process. In particular it can be deduced from these shapes when a trajectory is close enough to the boundary of an  $\mathbb{A}_k$  for a sufficiently large step to cause evolutionary pruning.

After evolutionary branching from  $\mathbb{A}_1$  into  $\mathbb{A}_2$  the trajectory the evolutionary path follows can be deduced by embedding  $\mathbb{A}_2$  into the two hyperplanes  $\Delta_{1,3}^3$  and  $\Delta_{2,3}^3$  and then analyse how the invasion fitness function  $s_2(\tau_1, \tau_2; \nu)$  behaves on the two embeddings of  $\mathbb{A}_2$ . A change in the first trait of a dimorphic community  $(\tau_1, \tau_2)$  is determined by the sign pattern of  $s_2$  on  $\Delta_{1,3}^3$ , and similarly a trait substitution in the second trait is determined by the pattern on  $\Delta_{2,3}^3$ . The combination of these changes composes the evolutionary path the community follows in  $\mathbb{T}^2$ . To avoid making these combinations of informations coming from two different local

patterns it would be useful to have one space available in which conclusions on how the evolutionary path for a community  $\tau_1, \tau_2$  proceeds can be concluded from the local properties of a suitable function at  $(\tau_1, \tau_2)$ . Similar questions on combining information from diagonal hyperplanes to conclude how an evolutionary path proceeds, and overcoming this by means of a suitable representation of course also hold for evolutionary paths in any  $\mathbb{A}_k, k \geq 2$ .

A next question deals with the relation between the function  $s_1$  and the evolutionary trajectories that it allows. What properties must  $s_1$  or, more precisely, the per capita initial growth function  $r$  and the interaction function  $a$  of a Lotka-Volterra model, satisfy to enable an evolutionary trajectory with an arbitrary number of branches, or with a specified number of branches?

A forthcoming paper will discuss bifurcation theory for adaptive dynamics based on Lotka-Volterra community dynamics. This bifurcation theory studies in particular if a IESS can change into an evolutionary branching point due to changes in the values of community-dynamical parameters that appear in the interaction function  $a$  and the per capita initial growth function  $r$  as they appear in the Lotka-Volterra differential equations in the previous chapter. The bifurcation theory gives insight in the way the set  $\mathbb{A}_2$  is attached to the 1- and 2-isoclines when one moves along these isoclines, i.e., about how the local shape of  $\mathbb{A}_2$  deforms along these isoclines.





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### Strategiedynamica

#### INLEIDING

Dit proefschrift bestudeert het begrip strategie met behulp van wiskundige modellen vanuit twee perspectieven. Het eerste deel behandelt de opiniedynamica. Hierin wordt geanalyseerd hoe de steun voor opinies verandert onder invloed van herhaaldelijke ontmoetingen tussen individuen met verschillende opinies. Deel 2 van het proefschrift bestudeert de veranderingen in strategieën als gevolg van evolutie.

#### OPINIEDYNAMICA

Opeenvolgende opiniepeilingen zoals die bijvoorbeeld plaatsvinden voorafgaand aan politieke verkiezingen laten vaak een verandering in steun aan opinies zien: de steun voor een of meerdere opinies neemt bijvoorbeeld toe ten koste van de steun aan alternatieve opinies, of de opinie die de meerderheid heeft is bij een volgende peiling vervangen door een andere opinie. Opiniedynamica beoogt door het construeren van wiskundige modellen inzicht te krijgen in het gedrag van steun aan opinies in de loop van de tijd, en met behulp van deze modellen voorspellingen te kunnen doen over dit gedrag.

In dit proefschrift worden twee modellen voor opiniedynamica onderzocht, waarbij het aantal opinies wordt beperkt tot twee, hier aangegeven met  $A$  en  $B$ . Hierbij kan gedacht worden aan de onderverdeling tussen 'links' en 'rechts' voor politieke partijen die onderling in opvattingen verschillen maar die ieder afzonderlijk in een van deze beide kampen onder te brengen zijn, of aan de onderverdeling van het politieke spectrum in de Verenigde Staten in republikeinen en democraten. In beide modellen worden de opiniedragers herhaaldelijk verdeeld in groepen, en afhankelijk van het type opiniedrager dat een groepslid is zal hij of zij wel of niet van opinie veranderen. In hoofdstuk 2 wordt voor de grootte van de groep 3 genomen (de kleinste groepsgrootte waarin voor twee opinies een meerderheid kan optreden); in hoofdstuk 3 worden eerst groepsgrootten 1 en 2 bestudeerd ter inleiding op het interessantere geval van groepsgrootte 3.

In hoofdstuk 2 wordt verondersteld dat voor beide opinies de aanhangers zijn onder te verdelen in zgn. *onbuigzamen* (of onwrikbaren; in het Engels *inflexibles* genoemd) en *zwevers* (floaters in het Engels). Een onbuigzame aanhanger van een opinie is iemand die onder alle omstandigheden bij deze opinie blijft en nooit van opinie zal veranderen. Een zwever daarentegen zal van opinie veranderen wanneer deze opinie de minderheid heeft in de groep waarin de zwever zich bevindt, en volgens het principe van de zgn. *locale meerderheidsregel* een zwever worden die de opinie ondersteunt die de meerderheid heeft in de groep. In hoofdstuk 3 wordt m. b. t. een zwever onderscheid gemaakt tussen een *tegendraadse zwever* (contrarian floater) en een *niet-tegendraadse zwever* (non-contrarian floater; in feite zijn de zwevers in hoofdstuk 2 allen niet-tegendraadse zwevers). Een tegendraadse zwever zal na het toepassen van de locale meerderheidsregel in de groep waarin deze zwever zich bevindt van opinie veranderen en een zwever voor de alternatieve opinie worden; de niet-tegendraadse zwever behoudt de opinie die na het toepassen van de locale meerderheidsregel is aangenomen. (In geval van groeps grootte 2 in hoofdstuk 3 wordt er neutraliteit aangenomen en behoudt een niet-tegendraadse zwever zijn of haar opinie; een tegendraadse zwever verandert wel van opinie.) Dit tegendraads gedrag van zwevende opiniedragers modelleert een houding die bijv. voorkomt bij individualistische adolescenten, i.h.b. in een omgeving waaraan hardnekkig wordt vastgehouden aan bepaalde opvattingen, bij verzet tegen de opinie met de meerderheid, of bij individuen die zich conformeren met de minderheid. Tegendraads gedrag van zwevers werd geïntroduceerd als mogelijke verklaring voor het kleine verschil in stemmen uitgebracht aan de twee kandidaten G. W. Bush en A. Gore tijdens de presidentsverkiezingen in de VS van 2000 (en heeft waarschijnlijk ook een rol gespeeld bij de presidentsverkiezingen in 2020).

Na toepassing van de locale meerderheidsregel gevolgd door de verandering van opinie door de tegendraadse zwevers (indien aanwezig) worden de opiniedragers opnieuw verdeeld over groepen (van steeds dezelfde grootte), waarna de opiniedragers in iedere groep opnieuw hun opinie bepalen. Voor de groepsvorming wordt steeds aangenomen dat iedereen in de gemeenschap een opinie heeft en dat de gemeenschap voldoende groot is, zodat het voorkomen van een bepaalde groepssamenstelling kan worden afgeleid uit de dichtheden van de onbuigzamen en (tegendraadse en niet-tegendraadse) zwevers in de gemeenschap. Na verloop van tijd zal in het algemeen een van beide opinies de meerderheid krijgen, maar welke dit is zal afhankelijk zijn van de dichtheden van onbuigzamen en zwevers in de gemeenschap en mogelijk van de beginsituatie.

In hoofdstuk 2 wordt aangetoond dat in afwezigheid van onbuigzamen voor beide opinies de opinie die aanvankelijk de meerderheid heeft deze meerderheid zal vergroten en de hele gemeenschap zal overnemen. Als er slechts van één van de twee opinies, zeg opinie A, onbuigzamen in de gemeenschap aanwezig zijn

met een aandeel in de totale gemeenschap dat lager is dan (ongeveer) 17%, dan hangt het van de samenstelling van de beginsituatie af welke opinie uiteindelijk de meerderheid krijgt: bij een voldoende grote aanvangsdichtheid van opinie *B* zal deze opinie de meerderheid bereiken en behouden, maar als opinie *A* bij aanvang in voldoende grote dichtheid aanwezig is zal *A* de gemeenschap volledig overnemen. Bij een aandeel van onbuigzamen voor *A* van minstens 17% zal opinie *B* altijd uit de gemeenschap verdwijnen (onafhankelijk van de beginsituatie).

Als het aandeel onbuigzamen voor opinie *A* groter is dan voor opinie *B* maar met een voldoende klein verschil tussen deze dichtheden dan zijn er twee coalities van beide opinies mogelijk: een coalitie waarin opinie *B* de meerderheid heeft en de andere waarin opinie *A* de meerderheid heeft, en het hangt weer van de beginconditie af welke opinie uiteindelijk de meerderheid zal krijgen. Als het verschil tussen dichtheden voldoende groot wordt in het voordeel van opinie *A* dan is er één enkele coalitie mogelijk waarin opinie *A* de meerderheid heeft. In het algemeen is de opinie die gesteund wordt door de grootste dichtheid aan onbuigzamen in het voordeel om uiteindelijk de meerderheid te bereiken in de gemeenschap.

In de opinie dynamica voor onbuigzamen en (niet-tegendraadse) zwevers worden de uiteindelijke dichtheden zgn. *monotoon* bereikt, waarbij een dichtheid van een opinie óf altijd kleiner óf altijd groter is dan de uiteindelijke dichtheid. Als er ook tegendraadse zwevers in de gemeenschap aanwezig zijn (hoofdstuk 3) is er naast *monotoon* gedrag ook *alternerend* gedrag mogelijk, waarbij beide opinies dichtheden aannemen die afwisselend kleiner en groter zijn dan de dichtheden die uiteindelijk in coalitie bereikt worden. Dit alternerende gedrag treedt bijvoorbeeld op als er voor beide opinies relatief lage dichtheden aan onbuigzamen aanwezig zijn en daarentegen hoge fracties tegendraadsen onder de zwevers. Als de uiteindelijke opinieverdeling zodanig is dat beide opinies met dichtheden van ongeveer 0.5 aanwezig zijn, kan zo'n scenario er toe leiden dat beide opinies op den duur nauwelijks in dichtheid van elkaar verschillen maar wel afwisselend de meerderheid hebben. Het exacte moment van verkiezing kan dan bepalend zijn welke opinie met nipte meerderheid wint. In het algemeen zal een toename in de fractie tegendraadsen onder de zwevers van een opinie tot een afname van de dichtheid van die opinie leiden in de coalitie die uiteindelijk bereikt wordt. Een opinie die in coalitie de meerderheid heeft kan deze dus behouden door de fractie tegendraadsen onder de zwevers beperkt te houden.

#### ADAPTIEVE DYNAMICA

In het deel over adaptieve dynamica verschuift de focus van dichtheden van strategieën naar het voorkomen van strategieën op de evolutionaire tijdschaal. In deze context wordt een strategie een fenotypisch kenmerk genoemd. Een

fenotypisch kenmerk is een eigenschap van organismen, zoals lichaamsgewicht, voedselkeuze, of een bepaalde vorm van gedrag. We beperken ons hier tot een strategie die middels een getalswaarde kan worden uitgedrukt. Dat zou bijvoorbeeld lichaamsgewicht kunnen zijn, of de maximale afstand waarover roofdieren een prooi kunnen ruiken. We zijn hier dus niet zozeer geïnteresseerd met welke dichtheden bepaalde waarden van een fenotypisch kenmerk in een gemeenschap voorkomen, maar welke waarden van dat kenmerk voorkomen en hoe veranderingen in die waarden wiskundig beschreven kunnen worden.

Om dit probleem te kunnen bestuderen worden er een aantal aannamen gedaan. We beschouwen een gemeenschap van populaties waarbij ieder individu aanwezig in een populatie dezelfde waarde heeft voor een niet nader gespecificeerd fenotypisch kenmerk, en waar de kenmerkwaarden tussen individuen van verschillende populaties van elkaar verschillen. De individuen in de gemeenschap zijn met elkaar in voortdurende competitie (bijvoorbeeld om voedsel of leefruimte), en de verschillende kenmerkwaarden bepalen de onderlinge competitieve sterkte. Er is dus competitie zowel tussen individuen binnen een populatie als tussen individuen van verschillende populaties. Na verloop van tijd zal de gemeenschap van populatie een stabiele modus van samenleven bereiken waarin de dichtheden van de populaties als gevolg van competitie mogelijk fluctueren in de tijd, maar waarin geen van de populaties zal uitsterven omdat sterfte van individuen binnen ieder van de populaties voldoende wordt gecompenseerd door geboorten. De populaties in deze stabiele modus worden de residente populaties genoemd, en de stabiele modus kan worden gerepresenteerd door de fenotypische kenmerkwaarden van deze residente populaties.

Als er ten gevolge van een mutatie in een van de residente populaties in stabiele modus een mutante populatie wordt voortgebracht, d.w.z. een populatie die in de waarde van het fenotypische kenmerk een geringe afwijking vertoont t.o.v. de moederpopulatie, dan kan met de gemeenschap van residente populaties en de mutante populatie als gevolg van competitie het volgende gebeuren:

- de mutante populatie redt het niet in competitie en zal verdwijnen, en de residente gemeenschap zal haar bestaan in stabiele modus voortzetten;
- de moederpopulatie zal als gevolg van competitie uitsterven omdat de individuen van de mutante populatie een iets betere competitieve sterkte hebben dan de individuen uit de moederpopulatie, en er wordt een nieuwe stabiele modus van samenleven bereikt door de overgebleven residente populaties en de mutante populatie;
- als gevolg van competitie zullen er meerdere populaties uit de gemeenschap uitsterven, en de populaties die overblijven komen uiteindelijk terecht in een nieuwe stabiele modus;

- de competitieve sterkte van de individuen in de mutante populatie is zodanig dat er een nieuwe stabiel modus van samenleven wordt bereikt van alle residente populaties met de mutante populatie.

Ter verduidelijking van het bovenstaande wordt hier opgemerkt dat het verschijnen van een mutante populatie met een kenmerkwaarde die de populatie in staat stelt om toe te nemen in dichtheid in competitie met de residente populaties relatief zeldzaam is. Het is daarom redelijk aan te nemen dat er slechts één mutante populatie door de residente populaties wordt voortgebracht, en dat de residente populaties als dit gebeurt inmiddels hun stabiele modus van samenleven hebben bereikt. De kenmerkende tijdsduur die populaties nodig hebben om een stabiele modus te bereiken bepaalt de gemeenschapsdynamische tijdschaal, en de kenmerkende tijdsduur die verloopt tussen het opeenvolgend verschijnen van mutante populaties die in dichtheden toenemen en in competitie gaan met residente populaties bepaalt de evolutionaire tijdschaal.

Voor de hierboven beschreven vier scenario's die mogelijk zijn na het verschijnen van een mutante populatie kan de uitkomst uitgedrukt worden door middel van de fenotypische kenmerken die aanwezig zijn in de uiteindelijk bereikte stabiele modus:

- in het eerste scenario zal er niets veranderen;
- in het tweede scenario wordt het kenmerk van de moederpopulatie vervangen door het kenmerk van de mutante populatie: er is sprake van een zgn. *kenmerksubstitutie*;
- het derde scenario zorgt voor een afname in het aantal kenmerken;
- het laatste scenario zorgt voor een toename in het aantal kenmerken met 1.

Wiskundig kan worden aangetoond dat het tweede scenario, waarbij een kenmerksubstitutie optreedt, de gebruikelijk gang van zaken is ten gevolge van het verschijnen van een mutante populatie in een residente gemeenschap. Als de kenmerkwaarden aanwezig in opeenvolgende stabiele modi worden uitgezet tegen de evolutionaire tijdschaal ontstaan er patronen die op bomen lijken: takken groeien als gevolg van kenmerksubstituties, en worden geknot bij afname in het aantal kenmerkwaarden, en vertakken als gevolg van een toename in het aantal kenmerkwaarden. (Zie hiervoor Figuur 1.1.)

In hoofdstuk 4, het eerste hoofdstuk in het deel over adaptieve dynamica, wordt de stabiele modus van samenleven van populaties wiskundig gedefinieerd. De wiskundige term die uitdrukking geeft aan deze modus is 'ep-chain attractor'. Een ep-chain attractor is een aanpassing van het chain-attractorbegrip van Ruelle voor een ecologische gemeenschapsdynamica, en heeft de eigenschappen die er op grond van ecologische processen redelijkerwijs aan gesteld mogen worden. In het bijzonder laat een ep-chain attractor niet toe dat een populatie die op de gemeenschapsdynamische tijdschaal uitsterft op deze tijdschaal weer

verschijnt en toeneemt in dichtheid. (Op de evolutionaire tijdschaal is dit echter wel mogelijk, als tenminste de juiste mutatie optreedt.)

In hoofdstuk 5 wordt voor een specifiek klasse van gemeenschapsdynamica (de klasse van Lotka-Volterra modellen) de zgn. *invasiefitness* voor een fenotypische kenmerkwaarde van een mutante populatie die verschijnt in een residente gemeenschap (in een ep-chain attractor) bepaald. Een positieve invasiefitness duidt op een toename in dichtheid van de mutante populatie (preciezer gezegd: op een positieve kans op toename van dichtheid), en een niet-positieve dichtheid duidt op het uitblijven van deze toename. Voor een mutante populatie die verschijnt in een enkele residente populatie worden de hierboven beschreven evolutionaire scenarios kenmerksubstitutie en vertakken (voor knotten zijn er minstens twee residente populatie nodig) geanalyseerd met behulp van de invasiefitness. Voor het geval dat de mutante populatie verschijnt in een residente gemeenschap met meerdere populaties worden noodzakelijke voorwaarden voor coexistentie van de mutante populatie met de residente populaties geformuleerd in termen van de invasiefitness.

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## CURRICULUM VITAE

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Frans Jacobs werd op 16 juli 1960 geboren in Asten. In 1979 behaalde hij het VWO-diploma aan het Serviam Lyceum in Sittard. In 1989 rondde hij zijn studie Wiskunde (met onderdelen uit de Theoretische Natuurkunde) af aan de Universiteit Utrecht. Zijn afstudeerscriptie had als onderwerp de classificatie van compacte vierdimensionale variëteiten.

Na zijn studie was hij enkele jaren als wiskundige verbonden aan de Vrije Universiteit in Amsterdam, waar hij meetkundig onderzoek deed aan het zgn. Hurwitz probleem voor kwadratische vormen. Vervolgens heeft hij de overstap gemaakt naar de theoretische biologiesectie van Hans Metz in Leiden om onderzoek te doen aan adaptieve dynamica. In adaptieve dynamica, dat beoogt de vorming van evolutionaire bomen te modelleren, komen diverse wiskundige disciplines samen met biologie: stochastische processen, dynamische systemen en meetkunde. Zijn voorkeur hierin ligt bij de wiskunde, in het bijzonder de meetkunde.

In 2001 werd Frans post-doc bij Prof. S. Gavrillets van The University of Knoxville in Tennessee om onderzoek te verrichten in de mathematische evolutionaire genetica. Na terugkeer uit de VS in 2003 heeft hij zijn werkzaamheden in de mathematische biologie in Leiden voortgezet. Daarnaast is hij onderzoek gaan doen aan opinie dynamica in samenwerking met S. Galam uit Parijs.

Momenteel is Frans als docent verbonden aan het Instituut voor Biologie van de Universiteit Leiden. Zijn onderwijs bestaat o.a. uit Basiswiskunde, Statistiek en de computerpractica Ecologie. Daarnaast is hij secretaris van de Prof. Dr. Jan van der Hoevenstichting voor Theoretische Biologie, en editor-in-chief van Acta Biotheoretica.



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