# Strategy dynamics

Jacobs, F.J.A.

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**Author**: Jacobs, F.J.A.
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# Introduction

# 1

# INTRODUCTION

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 repellor 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 repellor 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 repellors), 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[1]

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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[1] 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].

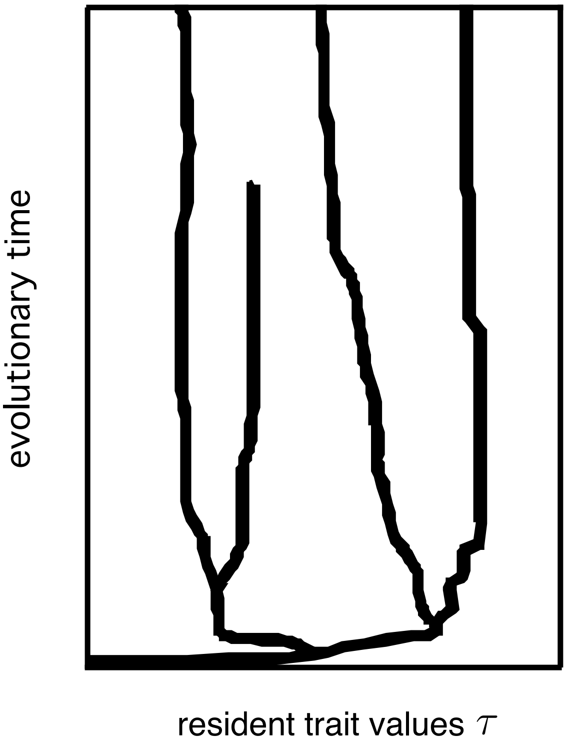

Figure 1.1: Phenotypic trait composition of subsequent community-dynamical attractors plotted against evolutionary time.

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.