universität wien

DIPLOMARBEIT

Titel der Diplomarbeit

Spatially structured games as an adaption of the Levene model

angestrebter akademischer Grad

Magister der Naturwissenschaften
(Mag. rer. nat.)

Verfasser:	Sebastian Novak
Matrikel-Nummer:	0401373
Studienrichtung:	A405 Mathematik
Betreuer:	Univ.-Prof. Dr. Josef Hofbauer

Wien, im Juli 2010

Without this playing with fantasy no creative work has ever yet come to birth. The debt we owe to the play of the imagination is incalculable.

Carl Gustav Jung
1875-1961, Swiss Psychiatrist

Abstract

This paper is concerned with a generalization of the Levene model (see H. Levene, [10]) in the context of game theory. More precisely we study symmetric normal form games with locally varying payoffs. After a rather heuristic derivation of our equations, we embed the model into a proper mathematical framework in the first chapter and make it clear to which extent the proposed generalization translates into known formulas. We conclude Chapter 1 with some basic theory on dynamical systems, which will be used in later sections. Chapter 2 is dedicated to the case of two strategies. The original question is whether or not our model allows for more dynamical scenarios than the Levene model. As a central point we answer an open problem by establishing that for two alleles and J habitats up to $2J-1$ interior fixed points may occur. Based on this result we can show that concerning the possible number of fixed points and the (generic) stability configurations indeed no new possibilities arise.
Proceeding one step further we arrive at the case of three strategies in Chapter 3. To obtain feasible results we confine to cyclic games, which have thoroughly been analyzed in panmictic models. For that specification explicit conditions for permanence of the system and for the stability properties of the (necessarily existent) interior fixed points can be derived. Furthermore, based on a result by C. Cannings [2], we show that for more than two strategies our generalization of Levene's model offers more dynamical opportunities than its archetype.
In the Appendix, the interested reader finds some supplementary results as well as the *Mathematica* program codes which were used to conduct simulations and create the figures in this paper.

Deutsche Zusammenfassung

Die vorliegende Arbeit befasst sich mit einer Verallgemeinerung des sogenannten *Levene Modells* (siehe H. Levene, [10]) in das Umfeld der Spieltheorie. Speziell interessieren wir uns für symmetrische Spiele in Normalform (Matrixform) mit regional unterschiedlichen Auszahlungen. Im ersten Kapitel leiten wir zuerst unser Modell heuristisch her und betten es anschließend in das entsprechende mathematische Umfeld ein um zu zeigen, inwiefern es mit bekannten Modellen überein stimmt. Den Abschluss von Kapitel 1 bildet ein kurzer Abriss über die Theorie dynamischer Systeme, auf die wir im Laufe der Arbeit zurückgreifen werden.

Das zweite Kapitel widmet sich dem Fall von zwei Strategien und stellt die Frage, ob unser Modell damit bereits mehr dynamische Möglichkeiten als das Levene Modell bietet. Im Mittelpunkt steht die Lösung eines offenen Problems: Wir zeigen, dass die theoretische obere Schranke an die Anzahl der inneren Fixpunkte angenommen werden kann. Davon ausgehend beweisen wir, dass die möglichen Anzahlen von Fixpunkten und die (generischen) Stabilitätskonfigurationen für beide Modelle die selben sind.

Als nächsten Schritt lassen wir im folgenden Kapitel drei Strategien zu. Um explizite Ergebnisse zu erhalten, beschränken wir uns hierbei auf zyklische Spiele, deren Verhalten ohne räumliche Struktur bereits gut analysiert wurde. Unter diesen Voraussetzungen treffen wir Aussagen über die Permanenz des Systems, sowie über die Stabilität des (notwendigerweise vorhandenen) inneren Fixpunktes. Ausgehend von der Arbeit von C. Cannings [2] zeigen wir weiters, dass unser Modell ab dem Vorhandensein von mindestens drei Strategien tatsächlich mehr dynamische Möglichkeiten als Levenes Original bietet.

Im Anhang findet der interessierte Leser außerdem ergänzende Resultate, sowie die *Mathematica*-Befehle, mit denen Simulationen durchgeführt und die Bilder in dieser Arbeit erzeugt wurden.

Danksagung

Diese Seite möchte ich all jenen Personen widmen, die mich während meines Studiums im allgemeinen — beziehungsweise bei dieser Arbeit im speziellen — unterstützt, motiviert und zwischendurch auf andere Gedanken gebracht haben. Insbesondere richte ich mich hierbei an:

- Prof. Josef Hofbauer. Für einen Großteil meines (bio)mathematischen Wissens sowie für die einwandfreie Betreuung meiner Diplomarbeit mit Interesse, selbstverständlicher Hilfsbereitschaft und wissenschaftlichem Vorwärtsdrang, welcher mich in positivstem Sinne gefordert wie gefördert hat.

- Meine KollegInnen. Allen voran Ada Akerman, die für mich seit dem Beginn unseres Studiums eine verlässliche Stütze wie auch einen erfrischenden Gegenpol in vielerlei Hinsicht darstellt.

- Grzegorz Stopa. Obwohl es ihn an dieser Stelle vielleicht überrascht. Weil der direkte Weg eben nicht der kürzeste ist.

- Meine Eltern. Denn ohne die geht gar nichts — weder materiell noch abseits derartiger Bedürfnisse.

- *Fachfremde* Freunde. Mit Bernhard Seedoch als höchstem Repräsentanten. Weil es nicht immer nur ernst sein darf.

- Felizitas Moll. Für Unterstützung und Vertrauen, für unsere Gemeinsamkeiten und Unterschiede, und für so viele Dinge, die ich nicht in Worte fassen kann.

Sebastian Novak, am 4.7.2010

Contents

Chapter 1

Introduction

1.1 The model

Imagine a group of salesmen meeting at some dusty inn in any city at any time you may think of. They decide, each one for his own, to go out into the wide world at a venture and try their mercantile fortune somewhere abroad. Apart from the collection of goods they assemble for sale, other decisions have to be made; some may hire heavy guard to protect their lives and property, others could prepare banners and posters for advertising campaigns at their destinations, and so on. However, after leaving home they find themselves in different surroundings, where the chosen strategies have to prove their worth. Furthermore, some merchants might find themselves having picked out the same place to raise their business as some of their friends from home, so each strategy is not only checked against local circumstances but against competing agents in the respective region.
Having lost contact with all their friends but those trading in their neighborhoods, the salesmen learn much by observing each other, comparing each other's actions with the associated profit or loss. In peaceful regions it turns out to be a waste of resources having invested too much in protection, in crowded areas advertising becomes vital. Finally, after having sold their stock of goods, all of the salesmen travel back home to feed and provide for their families. And, of course, they meet again at some dusty inn. There

they decide, each one for his own, to go out into the wide world with their acquired knowledge and try their mercantile fortune somewhere abroad.

This is, of course, just a simple story not worth being told at the fireplace, but let us try to embed the scenario into a mathematical framework, more precisely into the framework of game theory. In contrast to basic examples, we are confronted with several games — all allowing for the same strategies — and the players are assigned to different games in each round. Yet the more usual approach is considering a game with spatial structure and migration; a single game with varying payoffs depending on the location of the players, so to speak. To be precise, we proceed as follows.
We are looking at a group (or population) of players, which is supposed to be large enough such that we may ignore stochastic fluctuations in the argumentation at hand. Each player may choose one out of n (pure) strategies from the set $\mathbb{S} = \{1, ..., n\}$ and by x_i we denote the proportion of agents using strategy i. The vector x bearing information about the population's composition with regard to these strategies is

$$x = (x_i)_{i=1}^n \in \Delta := \{x \in \mathbb{R}^n : x \geq 0,\ \sum_{i=1}^{n} x_i = 1\}.$$

To simulate migration, players are dispersed randomly over J patches (demes, niches) according to their sizes (proportions) $n_1, ..., n_J$, where $\sum_{j=1}^{J} n_j = 1$. (This assumption of randomness seems unfitting to our salesmen-example, but one has to compromise.) Each individual then obtains a payoff $f^{(j)}(x^{(j)})$, $j = 1, ..., J$, depending explicitly on the patch j it is located on as well as on $x^{(j)}$, the composition of other agents acting there. Having split up agents randomly we can drop the second, implicit dependence on the niche, as the population structure must be the same as before dispersal. Thus we arrive at payoff functions $f^{(j)}(x)$, $j = 1, ..., J$.
In the investigations to follow we assume them to be linear and therefore - in tradition of standard game theory - end up with

$$f^{(j)}(x) = A^{(j)}x \quad j = 1, ..., J$$

where $A^{(j)}$ denotes the payoff matrix for deme j. Consequently, an i-player's payoff in patch j is $(A^{(j)}x)_i = \sum_{k=1}^{n} a_{ik}^{(j)} x_k$.

Next we need a mechanism to get hold of the individuals' decisions to switch strategies. It is convenient to use a discrete analogon of the replicator dynamics, which is an imitation dynamics most commonly applied to model learning processes. The quality of a strategy is measured at the payoff it provides in the respective situation in comparison to the average payoff that has been achieved: The higher the strategy's payoff, the more likely the strategy will be chosen. In a single-patch model this leads to the difference equation

$$x_i' = x_i \frac{(Ax)_i}{xAx} = x_i \frac{\sum_{l=1}^{n} a_{il} x_l}{\sum_{l,k=1}^{n} a_{kl} x_l x_k}. \tag{1.1}$$

Since we just have to add up each patch's contribution to each strategy's frequency in our spatially structured model, we finally arrive at

$$x_i' = x_i \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x} = x_i \sum_{j=1}^{J} n_j \frac{\sum_{l=1}^{n} a_{il}^{(j)} x_l}{\sum_{l,k=1}^{n} a_{kl}^{(j)} x_l x_k}. \tag{1.2}$$

This recursion may look familiar to some readers, as it basically is the Levene model[1] used to analyze gene frequencies over time with migrating individuals. Since the model should reasonably map the simplex Δ to itself, we require all $A^{(j)}$ to be positive matrices. Note that they need not necessarily be symmetric, as generally assumed in matters of population genetics.

1.2 The mathematical background

The following sections present an introduction into spatially structured models, which are commonly used in population genetics. We limit ourselves to models of discrete time and space to cast light on the bigger picture in which our scenario is set up[2].

[1] see H. Levene [10] for details

[2] cf. T. Nagylaki [12]

1.2.1 Spatially structured models

The basic discrete migration-selection model to describe the change of gene frequencies considers the following life cycle, which can be translated into an action sequence for a spatially structured game.
From the point of view of population genetics we are interested in gene frequencies. Therefore let $p_i^{(j)}$ denote the frequency of allele $i \in \{1, ..., n\}$ in deme $j \in \{1, ..., J\}$. Furthermore one has to keep track of the deme sizes n_j, as they might change when individuals wander from one niche to the other. Starting out at an initial state $(n_j, p_i^{(j)})$, reproduction leads to a new generation of zygotes, which experience selection when growing up. That entails a new set of gene frequencies $p_i^{(j)*}$, which are usually determined by the same model we introduced in 1.1, now reading

$$p_i^{(j)*} = p_i^{(j)} \frac{(W^{(j)} p^{(j)})_i}{p^{(j)} W^{(j)} p^{(j)}}$$

for positive, symmetric fitness matrices $W^{(j)}$.
Also deme sizes may change by selection if there is competition between niches. In that case, the success of each deme, similar to what we had above, depends on the average fitness of individuals within the respective deme in comparison to the average fitness over all demes:

$$n_j^* = n_j \frac{p^{(j)} W^{(j)} p^{(j)}}{\sum_{k=1}^{J} n_k p^{(k)} W^{(k)} p^{(k)}}$$

This assumption of competition beween niches is called *hard selection.* In contrast to that, assuming no such competition, one is talking about *soft selection.* In that case we simply set $n_j = n_j^* \ \forall j \in \{1, ..., J\}$.

Knowing how to simulate selection we turn towards the mechanism of migration. To this end we define

- $\widetilde{m}_{jk}$ as the probability that an individual from deme j migrates to deme k and
- m_{kj} as the probability that an individual in deme k was in deme j

before migration.

We call $\widetilde{M} = (\widetilde{m}_{jk})$ and $M = (m_{kj})$ the *forward-* and *backward-migration matrix*, respectively. It is clear that these matrices are stochastic. With M given, one can easily compute gene frequencies after migration by

$$p_i^{(j)**} = \sum_{k=1}^{J} m_{jk} p_i^{(k)*}.$$

However, it seems more realistic to assume only $\widetilde{M}$ to be known. Fortunately, converting $\widetilde{M}$ into M is not too difficult. Supposing that individuals are not getting lost during migration we can write

$$n_j^{**} = \sum_{k=1}^{J} n_k^* \widetilde{m}_{kj}.$$

Another obvious equality is

$$n_j^* \widetilde{m}_{jk} = n_k^{**} m_{kj}.$$

Inserting the first into the second equation, we arrive at

$$m_{kj} = \frac{n_j^* \widetilde{m}_{jk}}{\sum_{j=1}^{J} n_j^* \widetilde{m}_{jk}},$$

so we have explicit formulas for $\widetilde{M}$ and consequently for $p_i^{(j)**}$.

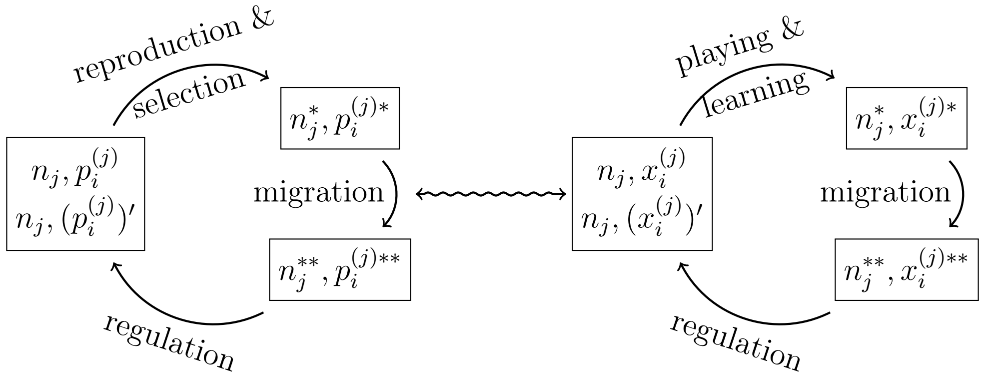
There is only one more problem yet to be solved: After migration some demes may be over- or underpopulated. Thus we need some regulation mechanism killing individuals which are exceeding niche sizes and filling up empty space in vacant places. Assuming that regulation hits all individuals the same (that is, regulation happens independently from the genotypes), gene frequencies are not affected. Thus $p_i^{(j)**} = p_i^{(j)'}$, while niche proportions are set back to their values before migration, i.e., $n_j' = n_j^*$. In other words we can skip computing n_j^{**}, which was needed to get a formula for $\widetilde{M}$ but does not directly influence the successive generation.

To summarize these results we can write down a difference equation which models the migration-selection process at hand. Because it is quite common, we assume *soft selection*. The equation reads

$$(p_i^{(j)})' = \sum_{k=1}^{J} m_{jk} p_i^{(k)*}, \tag{1.3}$$

where $m_{kj} = \frac{n_j \widetilde{m}_{jk}}{\sum_{j=1}^{J} n_j \widetilde{m}_{jk}}$ and $p_i^{(j)*} = p_i^{(j)} \frac{(W^{(j)} p^{(j)})_i}{p^{(j)} W^{(j)} p^{(j)}}$.

In order to adapt this model to our game theoretical background, one simply has to translate the reproduction and selection process into achieving a payoff by playing the game and changing strategies according to a learning mechanism. Regulation then means that redundant players drop out of the game and empty slots are populated by new participants. Furthermore we replace fitness information $W^{(j)}$ by (non-symmetric) payoff matrices $A^{(j)}$ as well as gamete frequencies $p_i^{(j)}$ by strategy distributions $x_i^{(j)}$. This leaves us with a neat identification



and we obtain

$$x_i^{(j)'} = \sum_{k=1}^{J} m_{jk} x_i^{(k)*} \tag{1.4}$$

where $m_{kj} = \frac{n_j \widetilde{m}_{jk}}{\sum_{j=1}^{J} n_j \widetilde{m}_{jk}}$ and $x_i^{(j)*} = x_i^{(j)} \frac{(A^{(j)} x^{(j)})_i}{x^{(j)} A^{(j)} x^{(j)}}$.

1.2.2 The Levene model

Obviously, (1.4) is still not the same thing as the model proposed in (1.2). In fact, we have not incorporated randomness of dispersal as supposed in Section 1.1. Considering this, we now go back to the framework of population genetics, where theis task has already been done by Howard Levene in 1953 (see [10]).

Assume that migration is independent from the niche of departure; this means, that for each deme $j \in \{1, ..., J\}$ we have a fixed number μ_j such that $\widetilde{m}_{kj} = \mu_j$ for all niches k. Naturally, we demand $\sum \mu_j = 1$.

Now we can calculate

$$m_{kj} = \frac{n_j \widetilde{m}_{jk}}{\sum_{j=1}^{j} n_j \widetilde{m}_{jk}} = \frac{n_j \mu_k}{\sum_{j=1}^{j} n_j \mu_k} = n_j^*$$

or, assuming *weak selection* from now on, $m_{kj} = n_j$. Furthermore, when looking at

$$(p_i^{(j)})' = \sum_{k=1}^{J} m_{jk} p_i^{(k)*} = \sum_{k=1}^{J} n_k p_i^{(k)*}$$

we assert that the right hand side of this equation does no longer depend on j. Thus it suffices to consider p_i instead of $p_i^{(j)}$; the state space of the model has become the $(n-1)$-dimensional simplex Δ. There is no geographic structure of the population per se, but selection varying regionally. The difference equation now reads

$$p_i' = p_i \sum_{j=1}^{J} n_j \frac{(W^{(j)}p)_i}{pW^{(j)}p} \tag{1.5}$$

which translates exactly into (1.2) when we apply the notation from our game theoretical framework.

1.2.3 Weak selection limit

When studying effects of selection in population genetics, selecting forces are usually very small. Introducing a parameter s for selection strength and letting $s \to 0$ one obtains the so-called *weak selection limit*, a system of ODEs that can be much easier to handle than the original difference equations. In context of game theory this procedure can be reasoned by looking at "unimportant" games; each player gets a certain *base payoff*, on which the game of interest only has little influence. The following lines present the weak selection limit for the spatially structured game model (1.2).

Normalizing the base payoff to 1 we rewrite payoff matrices $A^{(j)}$ by

$$a_{kl}^{(j)} = 1 + s r_{kl}^{(j)}$$

for $R^{(j)} = (r_{kl}^{(j)}) \in \mathbb{R}^{n \times n}$. Thus, as s becomes small, strategies will produce a similar payoff close to 1. Inserting in (1.2) we obtain

$$\begin{aligned} x_i' &= x_i \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x} \\ &= x_i \sum_{j=1}^{J} n_j \frac{1 + s(R^{(j)}x)_i}{1 + sxR^{(j)}x}. \end{aligned}$$

Then we calculate

$$\begin{aligned} x_i' - x_i &= x_i \left(\sum_{j=1}^{J} n_j \frac{1 + s(R^{(j)}x)_i}{1 + sxR^{(j)}x} - \underbrace{1}_{=\sum_j n_j} \right) \\ &= x_i \sum_{j=1}^{J} n_j \left(\frac{1 + s(R^{(j)}x)_i}{1 + sxR^{(j)}x} - 1 \right) \\ &= x_i s \sum_{j=1}^{J} n_j \frac{(R^{(j)}x)_i - xR^{(j)}x}{1 + sxR^{(j)}x}. \end{aligned}$$

Dividing by s we find

$$\frac{x_i' - x_i}{s} = x_i \sum_{j=1}^{J} n_j \frac{(R^{(j)}x)_i - xR^{(j)}x}{1 + sxR^{(j)}x}.$$

Now we set $x_i := x_i(t)$ and $x_i' := x_i(t + \Delta t)$. Also changing the timescale by

$\Delta t = s$ we let $s \to 0$ and arrive at

$$\frac{dx_i(t)}{dt} = x_i \sum_{j=1}^{J} n_j \left((R^{(j)}x)_i - xR^{(j)}x\right) \tag{1.6}$$

Defining a matrix R by $R := \sum_{j=1}^{J} n_j R^{(j)}$ we can write this as

$$\frac{dx_i(t)}{dt} = x_i \left((Rx)_i - xRx\right),$$

which is exactly the replicator dynamics commonly used to describe games in continuous time without spatial structure. One can say that a strategy will become more frequent, if taking the mean over all demes it does better than average. Thus in the limit of weak selection, the dynamics of equation (1.2) behaves as if there was no spatial structure. In fact, we expect (1.6) to approximate the system of difference equations (1.2) very well as long as all payoff values are sufficiently close to each other. Note, that we did not presume the matrices $R^{(j)}$ to be positive, but we allow for arbitrary $r_{kl}^{(j)} \in \mathbb{R}$.

1.3 Some theory on recurrence equations

1.3.1 Basic notions

In order to build up common vocabulary we skim through basic concepts and results concerning dynamical systems in discrete time. A first-order recurrence equation is a dynamical system given by

$$x_{t+1} = F(x_t), \tag{1.7}$$

where $F : M \to M$ is usually demanded to be at least continuous and M is some metric space (in our case, a subset of $\mathbb{R}^n$). For the sake of brevity we write (1.7) as

$$x' = F(x). \tag{1.8}$$

For $x_0 \in M$ we call the sequence

$$\{x_t\}_{t\geq 0} = \{F^t(x_0)|\ t \in \mathbb{N} \cup 0\}$$

the (forward) *orbit* of x_0 and x_0 is called the *starting point* of its orbit $\{x_t\}_{t\geq 0}$. A point $\widehat{x} \in M$ is a fixed point of (1.8), if $\widehat{x} = F(\widehat{x})$ holds true. Fixed points are said to be *stable*, if orbits near $\widehat{x}$ do not move far away. More precisely, a fixed point $\widehat{x}$ is stable if for any neighbourhood $U(\widehat{x}) \subset M$ we can find another neighbourhood $V(\widehat{x}) \subseteq U(\widehat{x})$, such that any orbit starting in $V(\widehat{x})$ remains in $U(\widehat{x})$ for all $n > 0$. If, additionally, nearby orbits even converge to $\widehat{x}$, $\widehat{x}$ is said to be *asymptotically stable* or an *attractor*. In case all orbits in a neighbourhood of $\widehat{x}$ move away from $\widehat{x}$, we call $\widehat{x}$ a *repellor*.

To decide about stability issues, the following theorem is of vital importance.

Theorem 1.3.1 (Hartman-Grobman)**.** *Let $x' = F(x)$ be a dynamical system with continuously differentiable $F : M \to M$, $M \subseteq \mathbb{R}^n$ open, and fixed point $\widehat{x}$. Furthermore, let $J := DF|_{\widehat{x}}$ denote the* linearization *of F and assume that $\widehat{x}$ is hyperbolic, i.e. for every eigenvalue λ of J we have $\lambda \neq 0$ and $|\lambda| \neq 1$. Then there are neighbourhoods $V \subseteq M$ of $\widehat{p}$ and $U \subseteq \mathbb{R}^n$ of 0 and a homeomorphism $\phi : V \to U$ such that $\phi \circ F = J \circ \phi$. Thus locally, F is topologically conjugate to its linearization J.*

This result tells us that, with the requirements from Theorem 1.3.1, the local stability properties of (1.8) in $\widehat{x}$ and of its linearization are qualitatively the same. Thus, if all eigenvalues λ_i of $J|_{\widehat{x}}$ fulfill $|\lambda_i| < 1$, $\widehat{x}$ is an attractor, whereas it is a repellor in case the opposite inequalities hold for all i. With mixed configurations, $\widehat{x}$ is some kind of saddle point.

1.3.2 ω-limits and Ljapunov functions

The concept of a *Ljapunov function* is a very powerful tool to analyze dynamical systems of any kind. Recall the following definitions.

Definition 1.3.2. *Let $x' = F(x)$ be a time-independent difference equation* *with continuous $F : G \to G$ for some $G \subseteq \mathbb{R}^n$. Furthermore let $\{x_t\}_t$ be a solution of this system with the initial condition $x_0 = x$.*

1. *The ω-limit of x is defined as*

$$\omega(x) := \{y \in \mathbb{R}^n : x_{t_k} \to y \ for\ some\ sequence\ t_k \to \infty\}$$

2. *The map $V : G \to \mathbb{R}$ is called a* Ljapunov function *for $x' = F(x)$ if V is continuous and for any $x \in G$ we have $V(x) \geq V(F(x))$.*

The theorem to come is analogous to the corresponding result in continuous time (see, e.g. Hofbauer and Sigmund [7], p.19).

Theorem 1.3.3. *Let V be a Ljapunov function for $x' = F(x)$ on G as above and $x \in G$. Then*

$$\omega(x) \cap G \subseteq \{x \in G : V(x) = V(F(x))\}$$

Proof. Assume $V(x) \geq V(F(x))$ for all $x \in G$. By induction it follows that $V(x_{t_1}) \geq V(x_{t_2})$ for $t_1 \leq t_2$ ($\diamond$).
Pick a $y \in \omega(x)$. By definition, a sequence $t_k \to \infty$ exists with $x_{t_k} \to y$.
Now suppose, that $V(y) > V(F(y))$.
We create another orbit $\{y_t\}_t$ with $y_0 = y$. In the first step V decreases and stays non-increasing from then on; thus we can conclude

$$V(y) > V(y_t) \tag{1.9}$$

holds for all $t > 0$.
From $x_{t_k} \to y$ by continuity of V we know that $V(x_{t_k}) \to V(y)$ and thus

$$V(x_t) \geq V(y)\ \forall t \in \mathbb{N}. \tag{1.10}$$

Applying F for t times on x_{t_k} and y, we get $x_{t_k+t} \to y_t$ and, again by continuity of V,

$$V(x_{t_k+t}) \to V(y_t).$$

Thus, $V(x_{t_k+t})$ comes arbitrarily close to $V(y_t)$ until, for t sufficiently large, we get by (1.9)

$$V(x_{t_k+t}) < V(y),$$

which is a contradiction to (1.10) by statement ($\diamond$). $\square$

1.3.3 Permanence

In the context of game theory, a dynamics $F : \Delta \to \Delta$ is called *permanent*, if no strategy can become extinct. More precisely, there must be an $\varepsilon > 0$ and an $t_0 = t_0(\varepsilon)$ such that for all starting vectors $x > 0$ we have $F^t(x) > \varepsilon$ for all $t > t_0$ and all $i = 1, ..., n$. We will give conditions for permanence of (1.2) with $n = 2$ and $n = 3$. The first case can be done easily without further theoretical background (see Section 2.3). To formulate a sufficient condition for the latter, we will need the following proposition, which is a special case of Corollary 2.3 by Hofbauer and So, [8], p.1139.

Proposition 1.3.4. *Let M be an invariant set of the system $x' = F(x)$, $F : X \to X$, and require that every ω-limit point in M is a fixed point of F. Furthermore let $X \setminus M$ be positively invariant. Then M is a repellor, if a continuous function $P : X \to \mathbb{R}^+$ exists, such that*

- *$P(x) = 0$ if and only if $x \in M$, and*
- *for every fixed point $\widehat{x}$ of $x' = F(x)$ in M we have $\psi(\widehat{x}) > 1$,*

where $\psi : X \to \mathbb{R}^+$ is defined by $P(F(x)) = \psi(x)P(x)$.

For our purposes we set $X = \Delta$ and $M = \partial\Delta$ and, by this proposition, have an instrument to check if orbits are pushed away from $\partial\Delta$ and thus no present strategy can get lost.

Chapter 2

The case of two strategies

Supported by the existence of a Ljapunov function the behaviour of the Levene model with two alleles has been analyzed quite well. Without this tool, the game theoretical model (1.2) is more difficult to handle.
Allowing for two strategies only, (1.2) is reduced to a single equation. Exploiting the fact that $x_1 + x_2 = 1$, we write $x := x_1$ (therefore $x_2 = 1 - x$) and only need to compute how x evolves. Writing the payoff matrices as

$$A^{(j)} = \begin{pmatrix} a_{11}^{(j)} & a_{12}^{(j)} \\ a_{21}^{(j)} & a_{22}^{(j)} \end{pmatrix}$$

equation (1.2) transforms into

$$x' = x \sum_{j=1}^{J} n_j \frac{a_{11}^{(j)} x + a_{12}^{(j)} (1-x)}{a_{11}^{(j)} x^2 + x(1-x)(a_{12}^{(j)} + a_{21}^{(j)}) + a_{22}^{(j)} (1-x)^2}. \tag{2.1}$$

2.1 Convergence to fixed points

At the beginning we assure ourselves of the fact that with two strategies present we will not be confronted with any complicated behaviour like periodic orbits or chaos, no matter how many demes might be interfering. In fact, every solution of (2.1) converges to a fixed point. This is based on the following result, which is well-known from the literature.

Proposition 2.1.1. *For continuous $F : \mathbb{R} \to \mathbb{R}$ consider the difference equation $x' = F(x)$. If F is monotonically increasing, every bounded orbit converges to a fixed point.*

Proof. Consider an orbit $\{x\}_{t=0}^{\infty}$ and suppose that $x_0 \leq x_1 = F(x_0)$. Because F is monotonically increasing we obtain by induction

$$x_t = F^t(x_0) \leq F^{t+1}(x_0) = x_{t+1}.$$

Hence $\{x_t\}_{t=0}^{\infty}$ is monotonically increasing and - if bounded - converges to a point $\widehat{x}$.
If $x_0 \geq x_1$, $\{x\}_{t=0}^{\infty}$ is monotonically decreasing due to the same argument. In any case, if the orbit is bounded, it converges to $\widehat{x}$.
Furthermore, $\widehat{x}$ must be a fixed point, as by continuity of F we have

$$\begin{aligned} x_t &\xrightarrow{t\to\infty} \widehat{x} \\ x_{t+1} = F(x_t) &\xrightarrow{t\to\infty} F(\widehat{x}), \end{aligned}$$

and from

$$\lim_{t\to\infty} x_t = \lim_{t\to\infty} x_{t+1}$$

we deduce $\widehat{x} = F(\widehat{x})$. □

Proposition 2.1.2. *Every orbit of (2.1) converges to a fixed point.*

Proof. To apply Proposition 2.1.1 we verify that F, denoting the right-hand side of (2.1), is monotonically increasing. We don't need to worry about unbounded orbits, as $F : [0,1] \to [0,1]$.
To simplify calculations we introduce a new variable by $z = \frac{x}{1-x}$.

$$\begin{aligned} F(z) &= z(1-x)\sum_{j=1}^{J} n_j \frac{a_{11}^{(j)} z(1-x) + a_{12}^{(j)}(1-x)}{a_{11}^{(j)} z^2(1-x)^2 + z(1-x)^2(a_{12}^{(j)} + a_{21}^{(j)}) + a_{22}^{(j)}(1-x)^2} \\ &= \sum_{j=1}^{J} n_j \frac{a_{11}^{(j)} z^2 + a_{12}^{(j)} z}{a_{11}^{(j)} z^2 + z(a_{12}^{(j)} + a_{21}^{(j)}) + a_{22}^{(j)}} =: \sum_{j=1}^{J} n_j \frac{(\diamond^{(j)})}{(\aleph^{(j)})} \end{aligned}$$

$$\frac{d}{dz}F(z) = \sum_{j=1}^{J} n_j \frac{\left(\aleph^{(j)}\right)\left(2a_{11}^{(j)}z + a_{12}^{(j)}\right) - \left(\diamond^{(j)}\right)\left(2a_{11}^{(j)}z + (a_{12}^{(j)} + a_{21}^{(j)})\right)}{\left(\aleph^{(j)}\right)^2}$$

Now it is not difficult to see that $\frac{d}{dz}F(z) \geq 0$ for all $z \in [0, \infty]$. Since the denominators do not cause us any trouble we simply check the numerators of each summand $j = 1, ..., J$.

$$\begin{aligned}
&\left(\aleph^{(j)}\right)\left(2a_{11}^{(j)}z + a_{12}^{(j)}\right) - \left(\diamond^{(j)}\right)\left(2a_{11}^{(j)}z + (a_{12}^{(j)} + a_{21}^{(j)})\right) = \\
&\quad = \left(2a_{11}^{(j)}z + a_{12}^{(j)}\right)\left(a_{21}^{(j)}z + a_{22}^{(j)}\right) - a_{21}^{(j)}\left(a_{11}^{(j)}z^2 + a_{12}^{(j)}z\right) = \\
&\quad = 2a_{11}^{(j)}a_{21}^{(j)}z^2 + 2a_{11}^{(j)}a_{22}^{(j)}z + a_{12}^{(j)}a_{22}^{(j)} + a_{12}^{(j)}a_{21}^{(j)}z - a_{11}^{(j)}a_{21}^{(j)}z^2 - a_{12}^{(j)}a_{21}^{(j)}z = \\
&\quad = a_{11}^{(j)}a_{21}^{(j)}z^2 + 2a_{11}^{(j)}a_{22}^{(j)}z + a_{12}^{(j)}a_{22}^{(j)} > 0,
\end{aligned}$$

which completes the proof. □

2.2 Qualitative equivalence to selection model

Without spatial structure the behaviour of the Levene model (1.5) and our game theoretical model (2.1) is qualitatively the same. This means, that allowing for asymmetric matrices does not give rise to new dynamical possibilities, which can be seen as follows.
Given a payoff matrix

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

we can always "transform" it into an admissible (i.e. symmetric) fitness matrix W. For that purpose, w.l.o.g. suppose $a_{12} - a_{21} \geq 0$ (otherwise relabel strategies accordingly), and add $c = a_{12} - a_{21} \geq 0$ to the first colum of A. The dynamics then becomes

$$x' = x\,\frac{(Wp)_1}{xWx} = x\,\frac{cx + (Ax)_1}{cx + xAx} =: \widetilde{F}(x). \tag{2.2}$$

Now assume that $\widehat{x}$ is a fixed point of the original equation

$$x' = x \, \frac{(Ax)_1}{xAx} =: F(x), \tag{2.3}$$

which means that $(A\widehat{x})_1 = \widehat{x}A\widehat{x}$. Inserting into (2.2), it becomes obvious that $\widehat{x}$ also is a fixed point of (2.2). Furthermore, the property of being attractor or repellor is the same under both equations: Calculating fixed points means intersecting F (or $\widetilde{F}$, respectively) with the line $y = x$. In regions where values of F lie above this function, i.e. $F(x) > x$ holds, we have an increase of x in the next generation and vice versa. Hence we can say that the dynamics of (2.3) and (2.2) qualitatively bear the same behaviour if the two functions

$$\begin{aligned} G(x) &:= F(x) - x \\ \widetilde{G}(x) &:= \widetilde{F}(x) - x \end{aligned}$$

have corresponding regions of positive and negative function values on $[0, 1]$. Since xAx (and thus also $cx + xAx$) is positive on this interval, we see that basically both functions are proportional to the same polynomial

$$p(x) := x \left((Ax)_1 - xAx \right).$$

Hence qualitatively (2.3) and (2.2) are the same. To make this precise, a different approach in the Appendix, Proposition 5.1.1, redrafts our finding and underlays the statement in a mathematically more profound way.

Clearly, this reasoning works out for $n = 2$ and $J = 1$ only. As soon as more strategies come into play, the argument above fails. Consider a cyclic game as proposed in Section 3.1. Then in general the matrix A from (3.1) cannot be transformed into a symmetric matrix by adding constants k_1, k_2 and k_3 to columns, because the equations

$$c + k_1 = b + k_2, \;\; b + k_1 = c + k_3, \;\; c + k_2 = b + k_3$$

do not necessarily have solutions for k_1, k_2 and k_3. Indeed, in Section 3.3.2

we find examples of (1.2) for $J = 3$, whose dynamics cannot be reproduced by (1.5).

If, on the other hand, spatial structure is introduced, adding constants to columns of the payoff matrices may symmetrize them but also change fixed points of the dynamics. Even with two demes, adding a constant $c > 0$ to, w.l.o.g., the first column of $A^{(1)}$ reduces the "importance" of the game in the first niche, because its contribution to the x_1-frequency in the new round changes from $x_1 n_1 \frac{(A^{(1)}x)_1}{xA^{(1)}x}$ to

$$x_1 n_1 \frac{cx + (A^{(1)}x)_1}{cx + xA^{(1)}x},$$

which is closer to the initial niche's contribution $x_1 n_1$. For $c \to \infty$, this expression even becomes $x_1 n_1$, transforming (1.2) into

$$x_1' = x_1 \left(n_1 + n_2 \frac{(A^{(2)}x)_1}{xA^{(2)}x} \right),$$

which has exactly the same fixed points as the panmictic model (1.1) with $A = A^{(2)}$, because

$$\begin{aligned} x_1 &= x_1 \left(n_1 + n_2 \frac{(A^{(2)}x)_1}{xA^{(2)}x} \right) \\ x_1 (1 - n_1) &= x_1 n_2 \frac{(A^{(2)}x)_1}{xA^{(2)}x} \\ x_1 &= x_1 \frac{(A^{(2)}x)_1}{xA^{(2)}x}. \end{aligned}$$

From this we conclude that fixed points in general change their position and for large c can even leave the area of interest when symmetrizing payoff matrices by the means above. Thus, at this point, we cannot exclude to find richer behaviour in (2.1) than in its counterpart from the field of population genetics. Nevertheless in Section 2.6 we will come back to this problem.

2.3 Conditions for permanence

As we will also do for the case of cyclic 3×3-games in Section 3.2.2, we investigate prerequisites on the payoff values to exclude the loss of any of the two strategies. With equation (2.1) being a one-dimensional problem, this reduces to calculating derivatives in $x = 0$ and $x = 1$.

Lemma 2.3.1. *Consider (2.1). Then strategy* 1 *is protected (i.e.,* $x = 0$ *is unstable) if*

$$\sum_{j=1}^{J} \frac{n_j a_{12}^{(j)}}{a_{22}^{(j)}} > 1. \tag{2.4}$$

Proof. Denoting the right hand side of (2.1) by $F^{(J)}(x)$ and setting $J = 1$ it is a simple computation to see that

$$\frac{dF^{(1)}}{dx}|_{x=0} = \frac{a_{12}^{(1)}}{a_{22}^{(1)}}.$$

Since taking the derivative is a linear operation, we obtain the proposed result. □

By relabeling strategies we find an analogous statement for strategy 2. Putting together these results we get a sufficient condition for permanence of the system.

Proposition 2.3.2. *The system (1.2) for* $n = 2$ *is permanent if both inequalities*

$$\sum_{j=1}^{J} \frac{n_j a_{12}^{(j)}}{a_{22}^{(j)}} > 1, \ \sum_{j=1}^{J} \frac{n_j a_{21}^{(j)}}{a_{11}^{(j)}} > 1 \tag{2.5}$$

hold true.

One might be interested in permanence for the case of equality in at least one of these formulas. For only two strategies, this question can be answered without notational difficulties. Let us call a fixed point $\widehat{x}$ of $x' = F(x)$, $F : \mathbb{R} \to \mathbb{R}$, *first-order neutrally stable*, if $\frac{dF}{dx}|_{x=\widehat{x}} = 1$. From Taylor expansion around $\widehat{x}$ up to order two we then obtain

$$|F(x)-\widehat{x}| = |F(x)-F(\widehat{x})| \approx |x-\widehat{x}| \left|1+\frac{x-\widehat{x}}{2}\frac{d^2F}{dx^2}|_{x=\widehat{x}}\right|.$$

Hence orbits near $\widehat{x}=0$ move away from that point if (2.4) holds or — in case of neutral stability — $\frac{d^2F}{dx^2}|_{x=0} > 0$. Analogously, suppose $\frac{dF}{dx}|_{x=0} = 1$ and $\frac{d^kF}{dx^k}|_{x=0} = 0$ for $k = 2, ..., m-1$; in that case, call $x = 0$ *neutrally stable of order* $m-1$. Then the first strategy is protected, if $\frac{d^mF}{dx^m}|_{x=0} > 0$.

We can apply this insight to our model (2.1), which has the form

$$x' = F(x) = xf(x).$$

The point $x = 0$ being first-order neutrally stable then translates into $f(0) = 1$. For the higher derivatives we find by induction

$$\frac{d^kF}{dx^k}|_{x=0} = k\frac{d^{k-1}f}{dx^{k-1}}|_{x=0},\ \ k \geq 1.$$

Thus, if $x = 0$ is neutrally stable of order k, one has to check the sign of $\frac{d^{k+1}F}{dx^{k+1}}|_{x=0}$ in order to make assertions about the protectedness of the first strategy. Unfortunately, going deeper into the matter by inserting the explicit formula for $f(x)$ entails work with many parameters and we have, so far, not been able to derive a feasible criterion for protectedness involving fitness parameters and niche proportions.

Note that for $J = 1$ the notion of neutral stability is nonrelevant, because $x = 0$ being neutrally stable excludes the existence of interior fixed points as well as neutral stability of $x = 1$. Hence in that case the sign of $\frac{df}{dx}|_{x=1} - 1$ co-determines the protectedness of $x = 0$.

2.4 The maximum number of fixed points

Even for the Levene model (1.5) with two alleles the exact greatest possible number of interior fixed points has not been assured yet. Solving the equation

		$i=0$	$i=1$	$i=2$	$i=3$	$i=4$	$i=5$
$J=2$	(1.5)	0.3866	0.5844	0.027	0.0021	–	–
	(1.2)	0.4629	0.5122	0.0234	0.0015	–	–
$J=3$	(1.5)	0.3496	0.6066	0.0393	0.0045	$1.4 \cdot 10^{-6}$	0
	(1.2)	0.4235	0.5389	0.0342	0.0034	$1.9 \cdot 10^{-6}$	0

Table 2.1: Approximate relative frequencies of cases with i interior fixed points for $n = 2$.

$x = F(x)$ (with F denoting the right-hand side of (1.5), $n = 2$) leads to the equation

$$0 = x(1 - x)R(x),$$

where R is some rational function whose numerator is a polynomial of degree $2J - 1$. Hence $2J - 1$ is an upper bound for the number of interior equilibria. For $J = 1, 2$ the situation is clear: Any possible number of fixed points with feasible stability configuration is known to occur in concrete examples. Furthermore, S. Karlin [9] found several examples for $J = 3$ producing four, as well as one configuration for $J = 7$ with five interior fixed points.

With our interest not being oriented towards the Levene model in the first place, but rather in its game theoretical counterpart (1.2), we asked ourselves at the beginning of this chapter if either model offers more dynamical possibilities than the other with increasing local division. Concerning the maximum number of fixed points we will use the following sections to first give concrete examples to answer this question for $J = 3, 4$. In the subsequent section we then present a general result (see also [13]).

2.4.1 Concrete examples

Table 2.1 displays the approximate frequencies of cases with i interior rest points for both (1.5) and (1.2), if $J = 2$ and $J = 3$, with randomly chosen payoff matrices and niche proportions. More precisely, for each row we created 10^7 payoff configurations by choosing payoff values uniformly $[0, 1]$-distributed. This is no restriction, because taking multiples of payoff matrices does not change the dynamics of the system. An algorithm following Sturm's Theorem about zeros of polynomials produced the number of fixed points for each configuration (the corresponding *Mathematica* code can be found in the Appendix, Program Code 5.2.1).

Reading from Table 2.1 one might doubt that the theoretical bound of 5 interior fixed points for $J = 3$ can be achieved. But consider the configuration

$$A^{(1)} = \begin{pmatrix} 1.29 & 9.17 \\ 4.15 & 2.26 \end{pmatrix}, \ A^{(2)} = \begin{pmatrix} 8.54 & 8.09 \\ 2.31 & 8.09 \end{pmatrix}, \ A^{(3)} = \begin{pmatrix} 1.02 & 0.47 \\ 2.45 & 8.39 \end{pmatrix}$$

and $n_1 = 0.0806$, $n_2 = 0.6857$, $n_3 = 0.2337$. Then equation (2.1) has fixed points at approximately

$$x_0 = 0, \ x_1 \approx 0.033, \ x_2 \approx 0.496, \ x_3 \approx 0.709, \ x_4 \approx 0.87, \ x_5 \approx 0.991, \ x_6 = 1,$$

and thus five interior fixed points, where x_1, x_3 and x_5 are asymptotically stable. For the purely symmetric case a very similar scenario can be produced. Setting

$$A^{(1)} = \begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}, \ A^{(2)} = \begin{pmatrix} 3 & 1 \\ 1 & 1 \end{pmatrix}, \ A^{(3)} = \begin{pmatrix} 1 & 1 \\ 1 & 3 \end{pmatrix},$$
$$n_1 = 0.26, \ n_2 = 0.37, \ n_3 = 0.37$$

equation (2.1) has fixed points at approximately

$$x_0 = 0, \ x_1 \approx 0.049, \ x_2 \approx 0.308, \ x_3 \approx 0.5, \ x_4 \approx 0.692, \ x_5 \approx 0.951, \ x_6 = 1,$$

where again x_1, x_3 and x_5 are asymptotically stable. The reverse stability configuration can be found in a similar example[1]:

$$A^{(1)} = \begin{pmatrix} 4 & 1 \\ 1 & 4 \end{pmatrix}, \ A^{(2)} = \begin{pmatrix} 25 & 1 \\ 1 & 1 \end{pmatrix}, \ A^{(3)} = \begin{pmatrix} 1 & 1 \\ 1 & 25 \end{pmatrix},$$

$$n_1 = 0.52, \ n_2 = 0.24, \ n_3 = 0.24$$

[1]Unlike in the panmictic model (1.1), one cannot replace $a_{ik}^{(j)}$ by $c - a_{ik}^{(j)}$, $c \in \mathbb{R}$ sufficiently large, to maintain fixed points but switch stability properties.

Inserting this into (2.1) produces equilibria at

$$x_0 = 0,\ x_1 \approx 0.205,\ x_2 \approx 0.328,\ x_3 \approx 0.5,\ x_4 \approx 0.672,\ x_5 \approx 0.795,\ x_6 = 1,$$

where, this time, x_0, x_2, x_4 and x_6 are asymptotically stable.

Pursuing this further, we can also give numerical examples for $J = 4$ with the greatest possible number of interior fixed points with all two generic stability configurations. The permanent scenario was created from the example above by introducing a fourth niche with small size but wide spread in payoff values. In the following tables, filled circles "•" represent stable fixed points, whereas unfilled rings "∘" stand for repellors.

$$A^{(1)} = \begin{pmatrix} 4 & 1 \\ 1 & 4 \end{pmatrix},\ A^{(2)} = \begin{pmatrix} 25 & 1 \\ 1 & 1 \end{pmatrix},\ A^{(3)} = \begin{pmatrix} 1 & 1 \\ 1 & 25 \end{pmatrix}, A^{(4)} = \begin{pmatrix} 1 & 100 \\ 100 & 1 \end{pmatrix},$$

$$n_1 = 0.51,\ n_2 = 0.24,\ n_3 = 0.24,\ n_4 = 0.01$$

0	0.003	0.16	0.446	0.5	0.554	0.84	0.997	1
∘	•	∘	•	∘	•	∘	•	∘

As for the reversed stability properties, we can present the following example:

$$A^{(1)} = \begin{pmatrix} 90 & 1 \\ 1 & 1 \end{pmatrix},\ A^{(2)} = \begin{pmatrix} 1 & 1 \\ 1 & 90 \end{pmatrix},\ A^{(3)} = \begin{pmatrix} 3 & 1 \\ 1 & 1 \end{pmatrix}, A^{(4)} = \begin{pmatrix} 1 & 1 \\ 1 & 3 \end{pmatrix},$$

$$n_1 = n_2 = 0.0564,\ n_3 = n_4 = 0.4436$$

0	0.126	0.329	0.443	0.5	0.557	0.671	0.874	1
•	∘	•	∘	•	∘	•	∘	•

2.4.2 A general construction

To simplify subsequent arguments, let us settle on the following notion.

Definition 2.4.1. *Let $x' = F(x)$ be a dynamical system on the interval $[0, 1]$. We call F (or the dynamics under F)* symmetric *if $F \circ \phi = \phi \circ F$ is a conjugacy for $\phi : x \mapsto 1 - x$ (that is, if $F(x) = 1 - F(1 - x)$ for all $x \in [0, 1]$).*

A simple observation gives

Lemma 2.4.2. *Let F_j, $j = 1, ..., J$, be symmetric and $\sum_j \varepsilon_j = 1$, $\varepsilon_j > 0$ $\forall j$. Then $\sum_j \varepsilon_j F_j$ is symmetric.*

Proof. This is obvious:

$$\sum_j \varepsilon_j F_j(x) = \sum_j (\varepsilon_j - \varepsilon_j F_j(1-x)) = 1 - \sum_j \varepsilon_j F_j(1-x)$$

$\square$

With this helpful tool at hand we start the following construction. Consider (1.2) for $n = 2$, which we write as

$$x' = \sum_{j=1}^{J} n_j f_j(x) =: F(x) \tag{2.6}$$

and suppose that

- F is symmetric,
- $x = 0$ and $x = 1$ are asymptotically stable, i.e. $\frac{d}{dx}F|_{x=0} < 1$, $\frac{d}{dx}F|_{x=1} < 1$, and
- F has k hyperbolic, interior fixed points[2] . We label them

$$0 < x_1 < ... < x_k < 1$$

Note that under these conditions two adjacent fixed points always must have different stability properties.

For $\zeta \geq 1$ define the following two matrices

$$Z^{(1)} = \begin{pmatrix} \zeta & 1 \\ 1 & 1 \end{pmatrix}, \; Z^{(2)} = \begin{pmatrix} 1 & 1 \\ 1 & \zeta \end{pmatrix}.$$

Then, if $0 < \varepsilon < 1$, the recursion

$$x' = (1-\varepsilon)F(x) + \varepsilon s(x) =: \widetilde{F}(x), \tag{2.7}$$

[2]That is, in every fixed point the absolute value of the derivative of F is $\neq 1$

where

$$s(x) = \frac{x}{2}\left(\frac{(Z^{(1)}x)_1}{xZ^{(1)}x} + \frac{(Z^{(2)}x)_1}{xZ^{(2)}x}\right),$$

defines a valid game in $J+2$ demes according to (1.2). The perturbation function s is symmetric and therefore, by Lemma 2.4.2, $\widetilde{F}$ is symmetric. Furthermore, s is continuous in ζ. Thus by choosing ε sufficiently small we can ensure that for all $\zeta \geq 1$ the new dynamical system (2.7) is *similar* to (2.6) in the following sense:

- Since s is bounded and monotone, all fixed points $\widetilde{x}_i$, $i = 1, ..., k$, of $\widetilde{F}$ are close to their original locations x_i. Furthermore, no other equilibria emerge and, in particular, none leave $[0,1]$.

- Since $s(0) = 0$, the point $x = 0$ remains a fixed point (and by symmetry of $\widetilde{F}$ the same holds for $x = 1$). Moreover these monomorphic states remain stable because

  $$\frac{ds}{dx}|_{x=0} = \frac{ds}{dx}|_{x=1} = \frac{1}{2}\left(1 + \frac{1}{\zeta}\right),$$

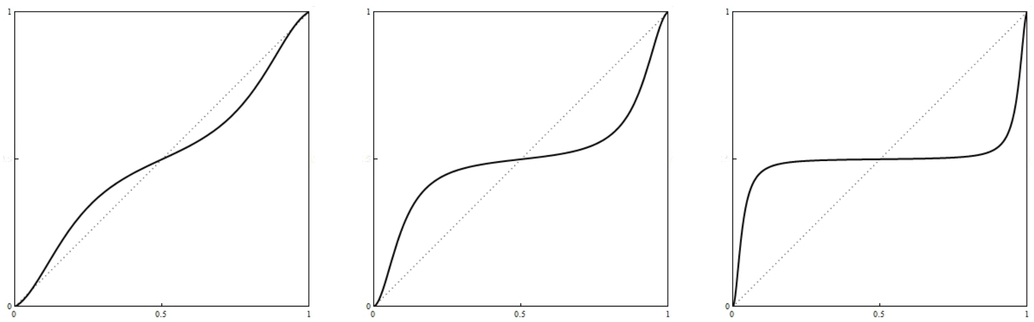
  which clearly is bounded for $\zeta \geq 1$.

- Because $\frac{ds}{dx}$ is uniformly bounded on every compact interval $[a, 1-a]$ ($0 < a < \frac{1}{2}$, see Lemma 5.1.2 (a) and (b)), $\frac{d\widetilde{F}}{dx}|_{x=\widetilde{x}_i}$ is close to $\frac{dF}{dx}|_{x=x_i}$ for ε small, uniformly in ζ. Hence the local stability properties of all equilibria $\widetilde{x}_i$, $i = 1, ..., k$, are maintained.

After a short calculation, we find $s(x) \to \frac{1}{2}$ if $\zeta \to \infty$ for all $x \in (0,1)$ (compare Figure 2.1), which motivates the next step:
Pick ε with $0 < \varepsilon < 2\widetilde{x}_1$ and $\delta \in (0, \frac{\varepsilon}{2})$. By the last statement we can find a $\zeta^* > 1$ such that

$$\delta < \varepsilon s(\delta) < \frac{\varepsilon}{2} < \widetilde{x}_1.$$

Therefore we have $\widetilde{F}(\delta) = (1-\varepsilon)F(\delta) + \varepsilon s(\delta) > \delta$ and $\delta \in (0, \widetilde{x}_1)$. From the stability configuration above we know that $\widetilde{F}(x) < x$ on a right-hand side neighbourhood $(0, \varepsilon_1)$ of 0 as well as on a left-hand side neighbourhood $(\widetilde{x}_1 - \varepsilon_2, \widetilde{x}_1)$ of $\widetilde{x}_1$. Thus by the intermediate value theorem it follows that two



(a) $\zeta = 20$ (b) $\zeta = 100$ (c) $\zeta = 1000$

Figure 2.1: The function s for some values of ζ. Note that $\frac{ds}{dx}|_{x=0} = \frac{ds}{dx}|_{x=0} < 1$ for all ζ which becomes visible only after zooming in.

more fixed points exist in $(0, \widetilde{x}_1)$. Since $\widetilde{F}$ is symmetric, we automatically have two additional equilibria in $(\widetilde{x}_k, 1)$ as well.

To sum up, we started out with a game in J niches with k fixed points and absorbing edges $x = 0$ and $x = 1$. We finally ended up with a dynamics with $J + 2$ niches and $k + 4$ fixed points. Note that we only used symmetric matrices so the procedure works for the Levene model (1.5) as well. This constitutes the proof of the following

Lemma 2.4.3. *Given an example of either (1.2) or (1.5) in J demes and k interior fixed points, where F is symmetric and $x = 0$ and $x = 1$ are asymptotically stable, we can always find a dynamics with $J + 2$ demes and $k + 4$ interior fixed points. This dynamics is symmetric and $x = 0$ as well as $x = 1$ are asymptotically stable.*

Now we have arrived where we wanted to get to:

Proposition 2.4.4. *For (1.2) (or (1.5), respectively) and $n = 2$ the theoretical upper bound of $2J - 1$ interior fixed points can be achieved. We may even confine to symmetric dynamics.*

Proof. Simple induction: For $J = 1, 2$ the configurations

$$A = \begin{pmatrix} 2 & 1 \\ 1 & 2 \end{pmatrix}, \left\{ A^{(1)} = \begin{pmatrix} 6 & 1 \\ 1 & 1 \end{pmatrix}, A^{(2)} = \begin{pmatrix} 1 & 1 \\ 1 & 6 \end{pmatrix}, n_1 = n_2 = \frac{1}{2} \right\}$$

give the required result. By repeatedly applying Lemma 2.4.3 we may construct examples with the maximum possible number of fixed points for any $J > 2$. $\square$

So far we only have a guarantee that examples with stable monomorphisms and a maximum possible number of fixed points — of which $J+1$ are stable — exist. The following proposition extends Proposition 2.4.4 to the case of protected alleles.

Proposition 2.4.5. *The theoretical upper bound of $2J-1$ interior fixed points in (2.1) for $n=2$ can be realized in permanent dynamics, i.e. with repelling monomorphisms.*

Proof. For $J = 1$ symmetric and permanent dynamics with one interior fixed point are known to exist (e.g., consider $A = \begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}$).
As in the argumentation leading to Lemma 2.4.3 take a dynamics F with J demes and attracting edges $x = 0$ and $x = 1$, which is symmetric and bears the maximum possible number $2J-1$ of interior fixed points. Consider equation (2.7) with

$$s(x) = x\frac{(Zx)_1}{xZx},$$

where $Z = \begin{pmatrix} 1 & \zeta \\ \zeta & 1 \end{pmatrix}$, $\zeta \geq 1$. Then again s is symmetric and $s(x) \to \frac{1}{2}$ on $(0,1)$ for $\zeta \to \infty$. Furthermore s is monotone and the derivative $\frac{ds}{dx}$ is uniformly bounded on every compact interval $[a, 1-a]$, $0 < a < \frac{1}{2}$ (consult the Appendix, Lemma 5.1.2 (c) for a proof of this statement). Therefore by choosing ε small and ζ large — for the things to come $\zeta > \frac{1}{\varepsilon}$ will suffice — we eventually obtain that all interior fixed points of F and their stability properties are maintained. In particular, $\widetilde{x}_1$ remains a repellor.
On the other hand $\frac{ds}{dx}|_{x=0} = \zeta$ and thus by the choice of ζ above we have

$$\frac{d\widetilde{F}}{dx}|_{x=0} = (1-\varepsilon)\frac{dF}{dx}|_{x=0} + \varepsilon\zeta > 0 + \varepsilon\frac{1}{\varepsilon} = 1.$$

Hence $\widetilde{x}_0 = 0$ is also a repellor and it follows that there is an additional rest point in $(0, \widetilde{x}_1)$. Because $\widetilde{F}$ is symmetric we automatically get another equilibrium in $(\widetilde{x}_{2J-1}, 1)$, and we have constructed a permanent dynamics with $J+1$ demes and $2J+1$ interior fixed points. $\square$

2.5 Even numbers of equilibria

By Lemma 2.4.3 and following the proof of Proposition 2.4.5 we immediately see that we can construct examples for any feasible configuration with an odd number of interior fixed points. In other words, for any $J \geq 1$ we can find a dynamics with $2k-1$, $k \in \{1, ..., J\}$, interior fixed points and preset stability properties ("*Repellor-attractor-...-attractor-repellor*" for the permanent case or "*attractor-repellor-...-repellor-attractor*"). To obtain an even number of interior fixed points we must get rid of the symmetry in our examples. Still the method is the same as conducted in Section 2.4.2.

As usual, suppose F to be a right-hand side of either equation (1.2) or (1.5) with $J \geq 1$ demes and $2k-1$ hyperbolic interior equilibria for some $k \in \{1, ..., J\}$. Furthermore presume that $x = 0$ and $x = 1$ are attractors. For $Z = \begin{pmatrix} 1 & \zeta \\ \zeta & \zeta \end{pmatrix}$, $\zeta \geq 1$, ε sufficiently small and $s(x) = x\frac{(Zx)_1}{xZx}$ consider equation (2.7). Lemma 5.1.2 (d) and some basic algebra show that

- s is monotone and $\frac{ds}{dx}$ is uniformly bounded in ζ on every compact interval $[a, 1-a]$, $0 < a < \frac{1}{2}$,
- $\frac{ds}{dx}|_{x=0} = 1$ and $\frac{ds}{dx}|_{x=1} = \zeta$.

By the first point we may assume (making ε smaller if necessary) that all interior fixed points and their stability properties are maintained. In particular, the rightmost interior equilibrium remains a repellor.
By the second point the property of $x = 0$ being an attractor remains unchanged as well. On the other hand, enlarging ζ we get arbitrarily large values for $\frac{ds}{dx}|_{x=1}$ — and hence also for $\frac{d\widetilde{F}}{dx}|_{x=1}$ — eventually making $x = 1$ a repellor. As we cannot have two repellors side by side, one additional (asymptotically stable) interior fixed point must have emerged.

Summing up we have a dynamics with $J+1$ demes and $2k$ ($k \in \{1, ..., J\}$) interior rest points. Putting this together with what we know from Section 2.4.2 (plus some bits of folklore to start inductive reasoning in a rigorous proof) we get:

Theorem 2.5.1. *If $n = 2$, both (1.2) and (1.5) allow for any number $k \in \{1, ..., 2J-1\}$ of interior fixed points with any feasible stability configuration.*

2.6 A final remark on equivalence

Let us turn back to the question remaining from Section 2.2: We already know that for $n = 2$ and $J = 1$ the equations (1.2) and (1.5) are equivalent in the sense that any dynamics induced by one model can be qualitatively reproduced by the other. After our findings in this section we know that for any $\widetilde{F}$, denoting a right-hand side of (1.5), we can find a right-hand side F of (1.2), such that F and $\widetilde{F}$ have the same number of fixed points with the same stability configuration. Hence we can apply Proposition 5.1.1 from the Appendix and find that there is a conjugacy between F and $\widetilde{F}$. Therefore we have shown:

Proposition 2.6.1. *If $n = 2$, (1.2) and (1.5) are equivalent in terms of none of them offering more dynamical possibilities than the other.*

Chapter 3

Cyclic games

3.1 Cyclic payoffs in a single patch

In preparation for the following chapters we will present basic results for a cyclic game without spatial structure. That means we are looking at the recurrence equation (1.1), which reads

$$x_i' = x_i \frac{(Ax)_i}{xAx}$$

and assume that A has the structure

$$A = \begin{pmatrix} a & b & c \\ c & a & b \\ b & c & a \end{pmatrix} \tag{3.1}$$

with $a, b, c > 0$.

3.1.1 A Ljapunov function

The following result was stated by J. Hofbauer in [5], p.771. As details are omitted there, we exercise the whole calculation.

Proposition 3.1.1. *The function* $V : \mathrm{int}\Delta \to \mathrm{int}\Delta$, $V(x) = \frac{xAx}{x_1 x_2 x_3}$, *is a Ljapunov function for the dynamical system (1.1).*

Note: The restriction to intΔ does not cause us any trouble, because $\partial\Delta$ (and thus also intΔ) is invariant under (1.1), which can be checked easily.

Proof. Clearly, V is continuous on intΔ.
We have to compare $V(x)$ with $V(x')$. For clarity, we first compute the average payoff after one generation:

$$x'Ax' = \sum_{i,j} a_{ij} x'_i x'_j = \sum_{i,j} a_{ij} x_i x_j \frac{(Ax)_i (Ax)_j}{(xAx)^2}$$

Introducing the notation $a_i := (Ax)_i$ and recalling that

$$A = \begin{pmatrix} a & b & c \\ c & a & b \\ b & c & a \end{pmatrix}$$

we can rewrite this as

$$x'Ax' = \frac{1}{(xAx)^2} \left(\underbrace{a \left(\sum_i x_i^2 a_i^2 \right) + (b+c) \left(\sum_i \sum_{j \neq i} x_i x_j a_i a_j \right)}_{\Theta} \right).$$

Hence we get for $V(x')$:

$$\begin{aligned} V(x') =& \frac{x'Ax'}{x'_1 x'_2 x'_3} \\ =& \frac{\Theta}{(xAx)^2} \cdot \frac{(xAx)^3}{x_1 x_2 x_3 a_1 a_2 a_3} \\ =& V(x) \frac{\Theta}{a_1 a_2 a_3} \end{aligned}$$

In order to establish that V is a Ljapunov function we have to make sure that $V(x') - V(x)$ never changes its sign, which is equivalent to $\Theta - a_1 a_2 a_3$ never changing its sign. To simplify calculations we introduce homogeneous coordinates by multiplying $a_1 a_2 a_3$ with $1 = x_1 + x_2 + x_3$. We obtain a homogeneous polynomial $T(x_1, x_2, x_3) = \Theta - a_1 a_2 a_3 (x_1 + x_2 + x_3)$ of degree four, which - after some strenuous manual work - turns out to have the form

$$T(x_1,x_2,x_3)=\left(a^2-bc\right)\left(a\cdot t_1(x_1,x_2,x_3)+b\cdot t_2(x_1,x_2,x_3)+c\cdot t_3(x_1,x_2,x_3)\right),$$

where

$$\begin{aligned}
t_1(x_1,x_2,x_3)&=x_1^4+x_2^4+x_3^4-x_1^2x_2x_3-x_1x_2^2x_3-x_1x_2x_3^2,\\
t_2(x_1,x_2,x_3)&=x_1^3x_2+x_2^3x_3+x_1x_3^3-x_1^2x_2x_3-x_1x_2^2x_3-x_1x_2x_3^2,\\
t_3(x_1,x_2,x_3)&=x_1x_2^3+x_1^3x_3+x_2x_3^3-x_1^2x_2x_3-x_1x_2^2x_3-x_1x_2x_3^2.
\end{aligned}$$

All this may look a little messy but it helps a lot that the polynomials t_1, t_2 and t_3 are non-negative on the simplex Δ. This can be seen quite easily: Obviously, the t_i are non-negative on $\partial\Delta$ because all summands with negative sign vanish if one x_i is zero. The usual procedure from differential calculus yields that all of the three functions (restricted on Δ) have a unique minimum at $\widehat{x}=(\frac{1}{3},\frac{1}{3},\frac{1}{3})$ with $t_1(\widehat{x})=t_2(\widehat{x})=t_3(\widehat{x})=0$. Hence all t_i and therefore also $at_1+bt_2+ct_3$ is nonnegative on the area of interest.
From the statement above it follows that the sign of T is determined only by the sign of a^2-bc, which does not depend on either of the x_i. Thus we have

$$V(x')\leq V(x)\ \forall x\in \mathrm{int}\Delta \text{ if } a^2<bc$$

$$V(x')\geq V(x)\ \forall x\in \mathrm{int}\Delta \text{ if } a^2>bc$$

with equality only at $\widehat{x}=(\frac{1}{3},\frac{1}{3},\frac{1}{3})$. If $a^2=bc$ holds, it follows that $V(x')=V(x)\ \forall x\in\mathrm{int}\Delta$, so all orbits move along level set curves of V. In any case we have shown that V is a Ljapunov function for (1.1). $\square$

3.1.2 Classification of behaviour

We are now able to sketch a rough picture of possible dynamics in cyclic 3×3 games. To this end, we first calculate the fixed points of (1.1). Apart from the trivial ones at the corners of Δ, i.e. where only one strategy is present, there is a unique interior fixed point at $P=(\frac{1}{3},\frac{1}{3},\frac{1}{3})$, the absolute minimum of the Ljapunov function V. As this is not obvious at first sight, the calculation is sketched in the Appendix, Lemma 5.1.3. From Proposition 3.1.1 we may conclude that for $a^2 < bc$ the fixed point P is globally stable. If $a^2 > bc$, all orbits starting in $\mathrm{int}\Delta$ move towards the boundary $\partial\Delta$.

To obtain information about behaviour at $\partial\Delta$, we treat local stability of $E_1 = (1,0,0)$, $E_2 = (0,1,0)$ and $E_3 = (0,0,1)$, the corners of Δ. For reasons of symmetry it is irrelevant which point to choose, so we decide for E_1. For the linearization we calculate:

$$\frac{\partial x_i'}{\partial x_k} = \delta_{ik}\frac{(Ax)_i}{xAx} + x_i\frac{xAx \cdot \frac{\partial}{\partial x_k}(Ax)_i - (Ax)_i \cdot \frac{\partial}{\partial x_k} xAx}{(xAx)^2} \tag{3.2}$$

Inserting E_1 we obtain the Jacobian

$$J|_{E_1} = \begin{pmatrix} 0 & -\frac{c}{a} & -\frac{b}{a} \\ 0 & \frac{c}{a} & 0 \\ 0 & 0 & \frac{b}{a} \end{pmatrix}.$$

The eigenvalues $\lambda_1 = \frac{b}{a}$ and $\lambda_2 = \frac{c}{a}$ of this matrix can be read from its diagonal[1]. Applying the Hartman-Grobman Theorem 1.3.1, we can summarize as follows (see also Figure 3.1[2]):

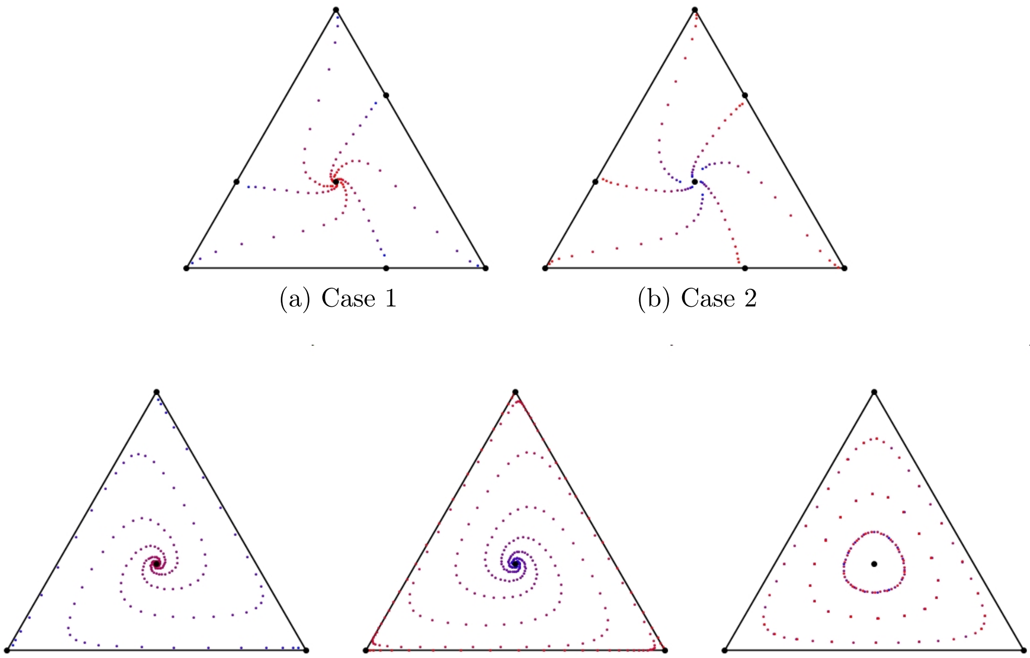
- **Case 1:** $b > a$ and $c > a$
  All orbits in the interior of Δ converge to $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$. Since the corners are repellors, we have an internally stable fixed point on each edge of Δ, i.e. stable coexistence of the strategies present.

- **Case 2:** $b < a$ and $c < a$
  The interior fixed point P is a repellor. Orbits of almost all starting values converge to one of the corners of Δ. This is a coordination game where it is best to act as the majority of the population does.[3]

[1] Ignoring the value zero belonging to an eigenvector transversal to Δ.

[2] For the corresponding *Mathematica*-code consult the Appendix, Program Code 5.2.2.

[3] *Remark*: This game produces the greatest possible number of seven *Nash equilibria* in (panmictic) 3×3-games. Besides the corners of Δ and P also the single fixed point at each edge of Δ is a Nash equilibrium.



(a) Case 1 (b) Case 2

(c) Case 3a (d) Case 3b (e) Case 3c

Figure 3.1: Classification of cyclic 3×3-games. Time evolving from blue to red.

- **Case 3:** w.l.o.g. $b > a$ and $c < a$
  The boundary of Δ forms a *heteroclinic cycle*: Each strategy dominates another and is dominated by the third in a cyclic way.

  - **Case 3a:** $a^2 < bc$
    In intΔ all orbits spiral towards P.
  - **Case 3b:** $a^2 > bc$
    In intΔ all orbits spiral away from P and towards $\partial\Delta$.
  - **Case 3c:** $a^2 = bc$
    As in this case we have $V(x) = V(x')$, all trajectories move along level sets of V. Hence each point in intΔ lies on an invariant closed curve around P.

3.2 Spatial structure with cyclic payoffs

Having done the preliminary work in the previous chapter we will now take account of a spatially structured population according to (1.2) with the additional assumption of cyclic payoffs in each deme. Thus we are investigating

$$x_i' = x_i \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x}$$

where

$$A^{(j)} = \begin{pmatrix} a^{(j)} & b^{(j)} & c^{(j)} \\ c^{(j)} & a^{(j)} & b^{(j)} \\ b^{(j)} & c^{(j)} & a^{(j)} \end{pmatrix}. \tag{3.3}$$

In what to come we first give conditions for the local stability of the interior fixed point and for permanence. These results are obtained by linearizing at the respective points and computing the absolute values of the corresponding eigenvalues.

3.2.1 Local stability of the interior fixed point

Before rushing right into stability issues we point out one simple but handy fact, which faciliates our work: As noted earlier, multiplying payoff matrices with a constant factor s does not affect the dynamics of (1.2), because s then appears both in enumerator and denominator and thus cancels out. We exploit that circumstance by rescaling our payoff matrices, in that case setting

$$a^{(j)} + b^{(j)} + c^{(j)} = 1 \qquad \forall j = 1, ..., J. \tag{3.4}$$

Furthermore we easily verify that $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is always a fixed point under (1.2) with payoffs according to (3.3). We sloppily address P as *the* interior fixed point of our model, although it need not be unique[4]. This is partially justified by the fact that the existence of more than one *isolated* interior fixed

[4]See Section 3.3.

point is yet doubtful.

Proposition 3.2.1. *The fixed point $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is stable under (1.2) with (3.3) and (3.4) if*

$$\left(\sum_{j=1}^{J} n_j a^{(j)}\right)^2 < \left(\sum_{j=1}^{J} n_j b^{(j)}\right)\left(\sum_{j=1}^{J} n_j c^{(j)}\right). \tag{3.5}$$

If the inverse inequality holds, P is a repellor.

Proof. We have

$$x_i' = x_i \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x} \qquad (i = 1, ..., n)$$

and need to compute the Jacobian at P. So we calculate

$$\begin{aligned} \frac{\partial x_i'}{\partial x_k} &= \delta_{ik} \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x} + \\ &+ x_i \sum_{j=1}^{J} n_j \frac{xA^{(j)}x \cdot \frac{\partial}{\partial x_k}(A^{(j)}x)_i - (A^{(j)}x)_i \cdot \frac{\partial}{\partial x_k} xA^{(j)}x}{(xA^{(j)}x)^2}. \end{aligned} \tag{3.6}$$

We are aimed at $\frac{\partial}{\partial x_k} x_i'|_P$. Let us check the components of that expression first:

$$\begin{aligned} &(A^{(j)}x)_i|_P = \frac{1}{3}(a^{(j)} + b^{(j)} + c^{(j)}) = \frac{1}{3} \\ &xA^{(j)}x|_P = \frac{1}{3}(a^{(j)} + b^{(j)} + c^{(j)}) = \frac{1}{3} \\ &\frac{\partial}{\partial x_k}(A^{(j)}x)_i|_P = (A^{(j)})_{ik} \\ &\frac{\partial}{\partial x_k} xA^{(j)}x|_P = \frac{2}{3}(a^{(j)} + b^{(j)} + c^{(j)}) = \frac{2}{3} \end{aligned}$$

We can summarize:

$$\frac{\partial}{\partial x_k} x'_i|_P = \delta_{ik} \sum_j n_j \frac{\frac{1}{3}}{\frac{1}{3}} + \frac{1}{3} \sum_j n_j \frac{\frac{1}{3}(A^{(j)})_{ik} - \frac{1}{3} \cdot \frac{2}{3}}{1/9}$$
$$= \delta_{ik} + \sum_j n_j (A^{(j)})_{ik} - \frac{2}{3} \tag{3.7}$$

The usual procedure to follow is to write down the Jacobian, calculate its eigenvalues and compute their absolute values. This entails strenuous work we can fortunately avoid, exploiting the simplicity of P. Define the matrix

$$H := \sum_{j=1}^{J} n_j A^{(j)}$$

and a single-niche model on Δ by

$$y'_i = y_i \frac{(Hy)_i}{yHy}. \tag{3.8}$$

Now we compute the Jacobian of (3.8) at P, which still is a fixed point of this altered dynamics. Adapting formula (3.2) from Section 3.1.2 we get:

$$\frac{\partial y'_i}{\partial y_k} = \delta_{ik} \frac{\sum_j n_j (A^{(j)} y)_i}{\sum_j n_j y A^{(j)} y} +$$
$$+ y_i \frac{\sum_j n_j y A^{(j)} y \cdot \sum_j n_j \frac{\partial}{\partial y_k} (A^{(j)} y)_i - \sum_j n_j (A^{(j)} y)_i \cdot \sum_j n_j \frac{\partial}{\partial y_k} y A^{(j)} y}{(\sum_j n_j y A^{(j)} y)^2}$$

Inserting P yields

$$\frac{\partial}{\partial y_k} y'_i|_P = \delta_{ik} + \frac{1}{3} \frac{\frac{1}{3} \sum_j n_j (A^{(j)})_{ik} - \frac{1}{3} \cdot \frac{2}{3}}{\frac{1}{9}}$$
$$= \delta_{ik} + \sum_j n_j (A^{(j)})_{ik} - \frac{2}{3},$$

which is exactly (3.7). Thus the local stability properties of P are the same under both dynamics (1.2) and (3.8). From Chapter 3.1 we transcribe the condition for stability of P, which produces the desired formula. $\square$

Remark 3.2.2. *As mentioned before, (3.4) means no restriction. We can get rid of this condition in (3.5) by dividing each payoff value by the sum* $a^{(j)} + b^{(j)} + c^{(j)}$. *(3.5) then reads*

$$\left(\sum_{j=1}^{J} \frac{n_j a^{(j)}}{a^{(j)} + b^{(j)} + c^{(j)}}\right)^2 < \left(\sum_{j=1}^{J} \frac{n_j b^{(j)}}{a^{(j)} + b^{(j)} + c^{(j)}}\right)\left(\sum_{j=1}^{J} \frac{n_j c^{(j)}}{a^{(j)} + b^{(j)} + c^{(j)}}\right).$$

3.2.2 Permanence

Thinking of the single-deme model (1.1) with cyclic behaviour induced by the payoff matrix (3.1), we remember from Section 3.1.2 that the eigenvalues of the linearization at the corners of Δ were $\lambda_1 = \frac{b}{a}$ and $\lambda_2 = \frac{c}{a}$. For (w.l.o.g.) $\lambda_1 > 1$ and $\lambda_2 < 1$, $\partial\Delta$ is a heteroclinic cycle. Taking $P(x) = x_1x_2x_3$ and applying Proposition 1.3.4, we see that it is repelling (or, equivalently, our system is permanent) if the product $\lambda_1\lambda_2 > 1$. As the calculation is straighforward, we omit it at this point and refer to the more general case we treat in the next proposition.

Proposition 3.2.3. *Consider the system of difference equations (1.2) on* Δ *with (3.3) and assume that there are no fixed points on* $\partial\Delta$ *apart from the corners of* Δ. *Then the system is permanent if*

$$\left(\sum_{j=1}^{J} \frac{n_j b^{(j)}}{a^{(j)}}\right)\left(\sum_{j=1}^{J} \frac{n_j c^{(j)}}{a^{(j)}}\right) > 1. \tag{3.9}$$

Proof. According to Proposition 1.3.4 we choose $P(x) = x_1x_2x_3$. It is easily verified that

$$P(x') = P(x) \prod_{i=1}^{3} \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x}.$$

Therefore

$$\psi(x) = \frac{P(x')}{P(x)} = \prod_{i=1}^{3} \sum_{j=1}^{J} n_j \frac{(A^{(j)}x)_i}{xA^{(j)}x}$$

and inserting any of the corners of Δ we get

$$\psi(\widehat{x}) = \prod_{i=1}^{3} \sum_{j=1}^{J} n_j \frac{(A^{(j)}\widehat{x})_i}{a^{(j)}}$$
$$= \underbrace{\left(\sum_{j=1}^{J} n_j \frac{a^{(j)}}{a^{(j)}}\right)}_{=1} \left(\sum_{j=1}^{J} n_j \frac{b^{(j)}}{a^{(j)}}\right) \left(\sum_{j=1}^{J} n_j \frac{c^{(j)}}{a^{(j)}}\right).$$

□

Remark 3.2.4. *Admittedly, the assumption of* having no fixed points at the edges of Δ *is not nice to work with. Unfortunately, it is difficult to give a handy formula for such points with more than one deme at hand, so we will stick to this rather vague statement. A necessary condition for $\partial\Delta$ being a heteroclinic cycle is $\lambda_1 \geq 1$ and $\lambda_2 \leq 1$ (or the other way round), where λ_i are the eigenvalues of the Jacobian at the corners of Δ. The following proposition gives explicit formulas for these values, which are basically transcribed from Section 2.3 and can be found again in (3.9).*

Proposition 3.2.5. *Consider the system of difference equations (1.2) on Δ with (3.3). Then the eigenvalues of the Jacobian of (1.2) at any of the points $E_1 = (1, 0, 0)$, $E_2 = (0, 1, 0)$ or $E_3 = (0, 0, 1)$ are*

$$\lambda_1 = \sum_j \frac{n_j b^{(j)}}{a^{(j)}}$$
$$\lambda_2 = \sum_j \frac{n_j c^{(j)}}{a^{(j)}}$$

Proof. Dealing with the dynamics on the edge $x_i = 0$ of Δ is equivalent to removing the i^{th} row and column from each payoff matrix and examining the recurrence equation for the remaining x_k, $k \neq i$. Thus following the argumentation leading to Proposition 2.3.2 produces the proposed formulas.

□

Remark 3.2.6. *Different from the case without spatial structure (see Section 3.1.2), the conditions for stability of P and for permanence of the system,* *(3.5) and (3.9), are not the same. We will, for example, investigate permanent systems with unstable fixed point P in the next section.*

3.3 Examples for possible behaviour

The following examples will demonstrate that even with relatively tough restrictions on the model (1.2), namely admitting only three strategies in two demes and assuming cyclic payoffs in each patch according to (3.3), we end up with interesting behaviour. We start out with known phenomena, namely

- continua of invariant curves, occurring already in the cyclic single-niche model (1.1)[5], and
- continua of fixed points, which can appear in the Levene model (1.5) as a special case of (1.2) requiring symmetric matrices $W^{(j)}$.

Introducing spatial structure or generalizing the payoff matrices, we ask ourselves if these properties can be reproduced using (1.2) with (3.3). This may give us a feeling how the cyclic single-niche model and Levene's model "combine" to our specific scenario.

3.3.1 Continua of invariant curves

As stated in Section 3.1.2, the cyclic single-deme model (1.1) yields a continuum of closed orbits if and only if $a^2 = bc$. At least for the case of two niches we will now work out a precise characterization of that behaviour for our case at hand. Initially, it might be conceivable that several niches balance in sophisticated ways, but the condition for a continuum of invariant curves turns out to be quite simple.
A necessary condition for intΔ consisting of closed orbits certainly is the interior fixed point as well as the boundary $\partial\Delta$ being neutrally stable. From

[5]See case 3c in Section 3.1.2.

Propositions 3.2.1 and 3.2.3 we conclude that

$$\left(\sum_{j=1}^{J} \frac{n_j a^{(j)}}{a^{(j)} + b^{(j)} + c^{(j)}}\right)^2 = \left(\sum_{j=1}^{J} \frac{n_j b^{(j)}}{a^{(j)} + b^{(j)} + c^{(j)}}\right)\left(\sum_{j=1}^{J} \frac{n_j c^{(j)}}{a^{(j)} + b^{(j)} + c^{(j)}}\right) \tag{3.10}$$

and

$$\left(\sum_{j=1}^{J} \frac{n_j b^{(j)}}{a^{(j)}}\right)\left(\sum_{j=1}^{J} \frac{n_j c^{(j)}}{a^{(j)}}\right) = 1 \tag{3.11}$$

must hold[6].

Now assume that we have only two niches with deme sizes n_1 and n_2. Similar to what we did in Section 3.2.1 we can rescale payoffs values, in this case setting $a^{(1)} = a^{(2)} = 1$. Thereby we can write condition (3.11) as

$$n_1 b^{(1)} + n_2 b^{(2)} = k$$

$$n_1 c^{(1)} + n_2 c^{(2)} = 1/k$$

for some real constant $k > 0$. Solving for $b^{(2)}$ and $c^{(2)}$ yields

$$b^{(2)} = \frac{k - n_1 b^{(1)}}{n_2}$$

$$c^{(2)} = \frac{1 - k n_1 c^{(1)}}{k n_2}.$$

Inserting in equation (3.10), we get after some basic algebra

$$b^{(1)} = \frac{1 - c^{(1)} k + k^2}{k}$$

and hence for $b^{(2)}$

$$b^{(2)} = \frac{k^2 - (1 - c^{(1)} k + k^2) n_1}{k n_2}.$$

[6]Note: As these conditions do not follow from $(a^{(j)})^2 = b^{(j)} c^{(j)}\ \forall j$, we cannot simply "add up" single niches bearing continua of closed orbits to get the desired effect.

Looking closer we see that

$$b^{(1)} + c^{(1)} = b^{(2)} + c^{(2)} \left(= k + \frac{1}{k} \right),$$

and because the average payoff in each niche can be written as

$$xA^{(j)}x = a^{(j)}(x_1^2 + x_2^2 + x_3^2) + (b^{(j)} + c^{(j)})(x_1x_2 + x_1x_3 + x_2x_3),$$

we end up with $xA^{(1)}x = xA^{(2)}x =: A(x)$ for all $x \in \Delta$.

As in the proof of Proposition 3.2.1 we now set

$$H := n_1A^{(1)} + n_2A^{(2)}.$$

Then $(Hx)_1 = n_1(A^{(1)}x)_i + n_2(A^{(2)}x)_i$ and $xHx = n_1 \cdot xA^{(1)}x + n_2 \cdot xA^{(2)}x = A(x)$. Thus we arrive at

$$\begin{aligned} x_i' &= x_i \left(n_1 \frac{A^{(1)}x)_i}{xA^{(1)}x} + n_2 \frac{A^{(2)}x)_i}{xA^{(2)}x} \right) \\ &= x_i \ \frac{n_1(A^{(1)}x)_i + n_2(A^{(2)}x)_i}{A(x)} \\ &= x_i \ \frac{(Hx)_i}{xHx}. \end{aligned} \tag{3.12}$$

Because (3.10) holds, we have case 3c from Section 3.1.2 at hand; that is, under system (3.12) $int\Delta$ consists of closed orbits. Hence (3.10) and (3.11) are a sufficient condition for the existence of a continuum of closed orbits and we have proved

Proposition 3.3.1. *For the case of two demes, $J = 2$, (1.2) with (3.3) provides a continuum of invariant curves around P if and only if conditions (3.10) and (3.11) hold.*

Allowing for more than two demes the calculations from above cannot be done that easily because too many variables are involved. Thus the average payoff being equal in every deme cannot be assured by the same arguments. Presuming $xA^{(1)}x = xA^{(2)}x = ... = xA^{(J)}x$, we can define $H := \sum_j n_jA^{(j)}$

and are able to rewrite (1.2) as (3.12). In that case, (3.10) ensures a continuum of invariant curves. So we can state:

Proposition 3.3.2. *If (3.10) holds and the average payoffs in each niche are the same for all $x \in \Delta$, then (1.2) with (3.3) provides a continuum of invariant curves.*

3.3.2 Continua of fixed points

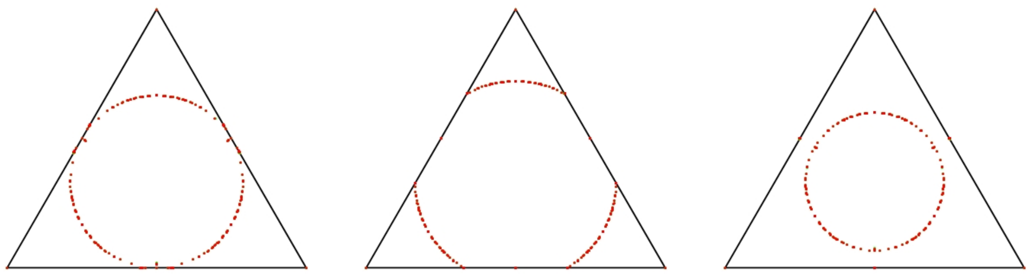
As C. Cannings [2] pointed out, continua of fixed points can occur even in the Levene model with two demes. The configuration

$$A^{(1)} = \begin{pmatrix} 1 & 2 & 2 \\ 2 & 1 & 2 \\ 2 & 2 & 1 \end{pmatrix}, \; A^{(2)} = \begin{pmatrix} 2 & 1 & 1 \\ 1 & 2 & 1 \\ 1 & 1 & 2 \end{pmatrix}, \; n_1 = n_2 = \frac{1}{2} \tag{3.13}$$

produces a dynamics with the incircle

$$x_1^2 + x_2^2 + x_3^2 - 2\left(x_1 x_2 + x_1 x_3 + x_2 x_3\right) = 0$$

of Δ consisting of fixed points. By slightly altering the niche proportions n_i one can easily shrink or enlarge this curve. Three numerical examples are given in Figure 3.2. These pictures were acquired by laying a grid of starting points over Δ and applying the generation map (1.2) with the above matrix configuration on them repeatedly. The respective program code is presented in the Appendix, Program Code 5.2.3. Just by the look of the pictures it is, of course, not clear that the depicted curves consist of fixed points, but following Cannings' reasoning we can overcome our doubts. For the complete argumentation we refer to the Appendix, Proposition 5.1.4.
For us this example is of interest, as it is a special case of a game with cyclic behaviour in each niche. To make it "*truly*" cyclic we added some cyclic perturbation in several ways, ending up with two qualitatively different results. While the first is presented in the following lines, we move the analysis of the second possibility to Section 3.3.3.



(a) $n_1 = n_2 = \frac{1}{2}$ (b) $n_1 = 0.48$, $n_2 = 0.52$ (c) $n_1 = 0.52$, $n_2 = 0.48$

Figure 3.2: Curves of fixed points in Cannings' example

Considering a single perturbation matrix

$$\Upsilon = \begin{pmatrix} 0 & \varepsilon & \delta \\ \delta & 0 & \varepsilon \\ \varepsilon & \delta & 0 \end{pmatrix}, \ \varepsilon > 0, \ \delta > 0$$

and the configuration

$$A^{(1)} + k\Upsilon, \ A^{(2)} - k\Upsilon, \ n_1 = n_2 = \frac{1}{2}, k \in \mathbb{R}, \tag{3.14}$$

simulations suggest that, depending on k, the curve of fixed points changes its diameter like it does in the pure symmetric scenario with varying niche proportions. The following proposition confirms this statement.

Proposition 3.3.3. *If* $1+2k(\delta+\varepsilon) > 0$*, the system (1.2) with (3.14) provides a continuum of fixed points, which is given by the intersection of* Δ *with the sphere centered around* $P = \left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$ *with radius* $r = \sqrt{\frac{1+2k(\delta+\varepsilon)}{3(2+k(\delta+\varepsilon))}}$.

Proof. Let $z = \left((s, -\frac{1}{2}\left(\sqrt{2-3s^2}+s\right), \frac{1}{2}\left(\sqrt{2-3s^2}-s\right)\right)$. Then $\sum z_i = 0$, $\|z\| = 1$ and $\gamma = P \pm rz$ defines a circle with radius r in the plane $(\mathbb{R}^3)_1 := \{x \in \mathbb{R}^3 : \sum x_i = 1\}$. Rewriting (1.2) as $x' = xf(x)$ we find

$$f(\gamma) = \frac{3}{2}\left(\frac{\alpha_1 P - rZ}{\alpha_1 - r^2\beta} + \frac{\alpha_2 P + rZ}{\alpha_2 + r^2\beta}\right),$$

where

$$\alpha_1 = 5 + k(\varepsilon + \delta), \;\; \alpha_2 = 4 - k(\varepsilon + \delta), \;\; \beta = 3\left(1 + \frac{k(\varepsilon + \delta)}{2}\right)$$

and $Z = z - k\varepsilon\overline{\overline{z}} - k\delta\overline{z}$. Here, $\overline{z}$ and $\overline{\overline{z}}$ are obtained from z by cycling through the vector's components. Inserting the formulas for r and z gives a lengthy expression which provides $f_i(\gamma) = 1$ for all $i = 1, 2, 3$. Thus every point on γ is a rest point.
The distance from P to either of the edges of Δ is $\sqrt{\frac{2}{3}}$. Therefore, for $\gamma \cap \mathrm{int}\Delta \neq \emptyset$ we require

$$r = \sqrt{\frac{1 + 2k(\delta + \varepsilon)}{3(2 + k(\delta + \varepsilon))}} < \sqrt{\frac{2}{3}}. \tag{3.15}$$

Suppose that $1 + 2k(\varepsilon + \delta) < 0$. Then $2 + k(\varepsilon + \delta) < 0$ must hold for γ to exist. Taking the square of (3.15) we get

$$1 + 2k(\varepsilon + \delta) > 4 + 2k(\varepsilon + \delta),$$

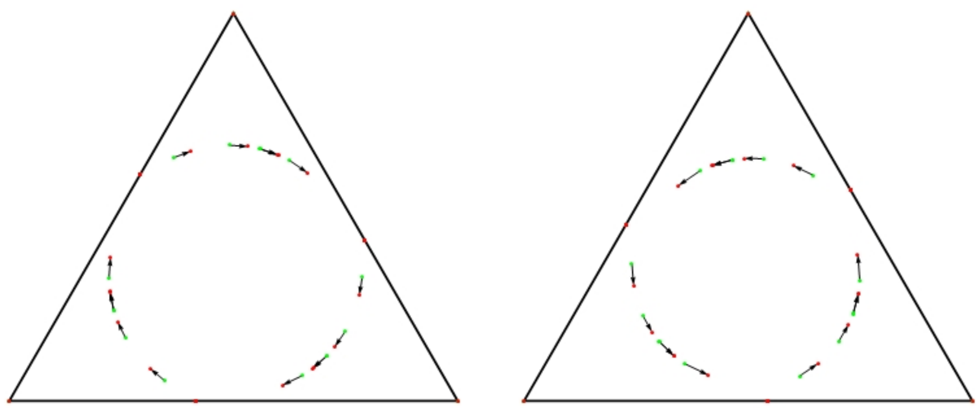
which is obviously untrue, hence γ is located outside of Δ.
From $1 + 2k(\varepsilon + \delta) > 0$ as proposed it follows that also $2 + k(\varepsilon + \delta) > 0$ and (3.15) becomes

$$1 + 2k(\varepsilon + \delta) < 4 + 2k(\varepsilon + \delta).$$

Thus under given conditions we have $\gamma \cap int\Delta \neq \emptyset$. □

3.3.3 Attracting curves

Apart from what we showed in the previous section, many other perturbations of (3.13) lead to a collapse of the fixed point manifold. In its place, simulations show an invariant curve, along which orbits move around the interior fixed point $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$. This definitely can not happen in the Levene model, as such a behaviour contradicts the existence of a (strict) Ljapunov function, which would have to be strictly monotone along a closed curve.



(a) $k = 0$, clockwise rotation

(b) $k = 2$, counterclockwise rotation

Figure 3.3: Change of rotational direction

As an example consider

$$A^{(1)} = \begin{pmatrix} 1 & 2+\varepsilon & 2+\delta \\ 2+\delta & 1 & 2+\varepsilon \\ 2+\varepsilon & 2+\delta & 1 \end{pmatrix}, \; A^{(2)} = \begin{pmatrix} 2 & 1+k\delta & 1+k\varepsilon \\ 1+k\varepsilon & 2 & 1+k\delta \\ 1+k\delta & 1+k\varepsilon & 2 \end{pmatrix},$$

with $\varepsilon, \delta > 0$, $\varepsilon \neq \delta$, $n_1 = n_2 = \frac{1}{2}$ and $k \geq 0$. Setting $\varepsilon = 0.02$, $\delta = 0.01$ and $k = 0$, simulations show clockwise rotations on an attracting curve, while e.g. for $k = 2$ the rotational direction is counter-clockwise (see Figure 3.3). To confirm that these simulations are not misleading we sketch a systematic analysis.

- The system is permanent.

Applying Proposition 3.2.5 we obtain $\lambda_1 = \frac{1}{4}(5 + 2\varepsilon + k\delta) > 1$ and $\lambda_1 = \frac{1}{4}(5 + 2\delta + k\varepsilon) > 1$ and therefore the corners of Δ are repellors. It follows that at least one fixed point on each edge of Δ must exist, hence we cannot apply Proposition 3.2.3. To see that the system is permanent, we proceed as follows:
W.l.o.g. we pick the edge $x_3 = 0$, which is repelling if $\frac{x_3'}{x_3} = f_3(x) > 1$ for $x_3 \approx 0$. By reasons of continuity we only need to show that $f\left((x, 1-x, 0)\right) > 1$

for $x \in (0,1)$ or, equivalently, $f((x, 1-x, 0)) - 1 > 0$. As the denominator of this expression is greater than zero, we need the numerator — which is a polynomial p of degree four — to be greater than zero as well for the system to be permanent. Immediately we get

$$p(0) = 1 + 2\delta + k\varepsilon,\ p(1) = 1 + 2\varepsilon + k\delta.$$

Assuming that ε and δ are small enough[7] to ignore terms of higher order in these parameters (i.e. ε^2, δ^2, $\varepsilon\delta$, ...), we find that p has a single critical point in $\mathbb{R}$ at

$$\overline{x} = \frac{1}{8}\left(4 + 3(k-1)(\varepsilon - \delta)\right)$$

with function value

$$p(\overline{x}) = \frac{1}{4}(1 + 2k)(\varepsilon + \delta) > 0.$$

Thus $p(x) > 0$ on $(0,1)$ and therefore the system is permanent.

- The interior fixed point $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is a repellor.

Inserting into (3.5) from Proposition 3.2.1 and expanding into a Taylor series around $\varepsilon = 0$ and $\delta = 0$ up to first order, we find that $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ is a repellor if $27 > (94 + 65k)\varepsilon + (70 + 65k)\delta$, which holds for sufficiently small ε and δ. Note that in the above numerical example this inequality is fulfilled. Together with the previous point this implies the existence of an attractor between P and $\partial\Delta$, which — in the absence of further fixed points — has the shape of a (distorted) annulus. Numerical simulations suggest that it takes the form of an invariant curve, but investigating the dynamics on this is a remaining problem.

- No further interior fixed points for almost every choice of parameters.

Verifying this statement rigorously is disproportionately hard work which can hardly be retraced without the extensive use of CAS. Here we will limit

[7] In the example given above, the values of ε, δ and k are within the admissible range for all arguments to follow.

ourselves to showing that, for almost every choice of parameters, there are no fixed points on the line $l(s) = (1-s, \frac{s}{2}, \frac{s}{2})$, $s \in (0,1)$ apart from P. This does not exclude the possibility of a heteroclinic attractor in intΔ, but on the one hand we would then observe great differences in the orbit's speed depending on its distance to the fixed points in this attractor (which in simulations we do not). On the other hand it would not change the message of this section, namely that we can give examples for which the dynamics of (1.2) is complicated enough to object the existence of a Ljapunov function for this model.

We are interested in solutions of

$$F\left(l(s)\right) = l(s),$$

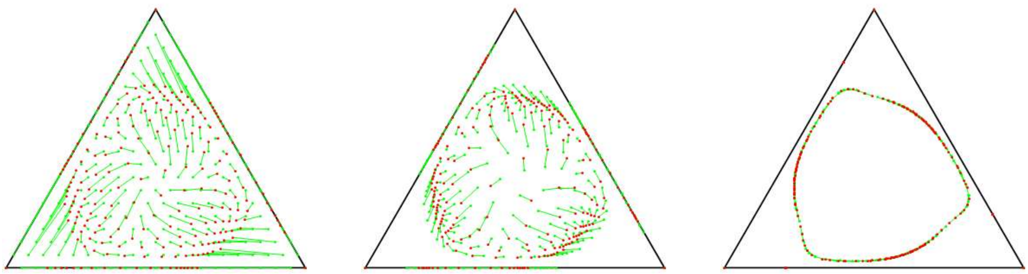
which means three equations in only one variable s (F stands for the right-hand side of (1.2) as usual). Solving $F_1\left(l(s)\right) = l_1(s)$ gives three solutions that are in $(0,1)$:

$$s_0 = \frac{2}{3},\ s_{1,2} = \frac{2}{3} \pm \frac{\sqrt{2}}{3}\sqrt{2 - \frac{3(2+(2+k)(\varepsilon+\delta))}{(2+\varepsilon+\delta)(2-k(\varepsilon+\delta))}}$$

We may ignore s_0 because it represents $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$. If the other values are fixed points, they must fulfill $F_2\left(l(s_{1,2})\right) = l_2(s_{1,2})$. Some direct computations yield

$$F_2\left(l(s_{1,2})\right) - l_2(s_{1,2}) = \left(1 - (1+\varepsilon+\delta)k\right)(\delta - \varepsilon)K,$$

where $K < 0$ as long as ε and δ are sufficiently small. Thus we only have further fixed points on the line l if $k = \frac{1}{1+\varepsilon+\delta}$. In that case one can show that again we have a continuum of fixed points; we will not exercise this. If k deviates from that value, there are no fixed points apart from P in intΔ. For $k < \frac{1}{1+\varepsilon+\delta}$ we then observe clockwise, for $k > \frac{1}{1+\varepsilon+\delta}$ counter-clockwise rotations.



(a) (b) (c)

Figure 3.4: Closed attracting curve and fixed points on $\partial\Delta$

3.3.4 A concluding example

The way we obtained the examples above and the fact that we had to take ε and δ sufficiently small has a somewhat artificial aftertaste. Anyhow, closed attracting curves can also be found in apparently generic (cyclic) games as the following configuration illustrates. Consider

$$A^{(1)} = \begin{pmatrix} 2.231 & 9.747 & 4.781 \\ 4.781 & 2.231 & 9.747 \\ 9.747 & 4.781 & 2.231 \end{pmatrix}, \; A^{(2)} = \begin{pmatrix} 8.729 & 0.156 & 5.573 \\ 5.573 & 8.729 & 0.156 \\ 0.156 & 5.573 & 8.729 \end{pmatrix}$$

and $n_1 = n_2 = \frac{1}{2}$. This example is of interest as the resulting dynamics shows two fixed points within each edge of Δ, a repelling interior fixed point and an attracting curve (see Figure 3.4). Thus, the variety of dynamical possibilities — even for the restriction on cyclic games — seems to pose a challenge with regards to eventual systematic classifications.

Chapter 4

Conclusion

To concludingly summarize our results we can state that one can generalize Levene's model without notational difficulties to the context of game theory. Unfortunately the convenient feature of having a Ljapunov function at hand does not hold true in our generalization, but conditions for the qualitative behaviour of the model have to be directly computed. We exercised this by giving explicit formulas for permanence of the system for the case of two strategies (Section 2.3) and for cyclic 3×3-games (Section 3.2.2). For the latter case we also established prerequisites on the local stability of the (always existent) interior equilibrium $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ (Section 3.2.1).
For $n = 2$ we showed that our proposed generalization of the Levene model is qualitatively equivalent to its archetype, so in fact allowing for asymmetric matrices does not increase the variety of dynamical situations opening up (Sections 2.2 and 2.6). On the way to this result we affirmed the open problem whether the theoretical upper bound on the number of equilibria can be attained for the Levene model with $n = 2$ (Section 2.4).
In the case of $n \geq 3$ the above equivalence clearly does not hold. We endorsed this statement by presenting a class of games ($n = 3,\ J = 2$) whose dynamics show invariant curves, which cannot happen in the Levene model (Section 3.3). In particular these examples contradict the existence of a strict Ljapunov function for our model.

Chapter 5

APPENDIX

5.1 Part I: Supplementary results

Proposition 5.1.1 (c.f. Section 2.2 and 2.6). *Consider two strictly increasing maps $F, \widetilde{F} : [0,1] \to [0,1]$ and assume that F has fixed points exactly at $\widehat{x}_i$, $i = 0, ..., k+1$,*

$$0 = \widehat{x}_0 < \widehat{x}_1 < ... < \widehat{x}_{k+1} = 1,$$

and that $\widetilde{F}$ has fixed points exactly at $\widetilde{x}_i$, $i = 0, ..., k+1$,

$$0 = \widetilde{x}_0 < \widetilde{x}_1 < ... < \widetilde{x}_{k+1} = 1.$$

Furthermore suppose that F and $\widetilde{F}$ induce the same stability configuration, i.e. for fixed $i \in \{0, ..., k\}$ and $x \in (\widehat{x}_i, \widehat{x}_{i+1})$, $\widetilde{x} \in (\widetilde{x}_i, \widetilde{x}_{i+1})$ we have

$$\operatorname{sgn}\big(F(x) - x\big) = \operatorname{sgn}\big(\widetilde{F}(\widetilde{x}) - \widetilde{x}\big).$$

Then the functions F and $\widetilde{F}$ are topologically conjugate via a homeomorphism $\Phi : [0,1] \to [0,1]$; that is, we have a homeomorphism Φ, such that the following diagram commutes:

$$\begin{tikzcd}
[0,1] \arrow[r, "F"] \arrow[d, "\Phi"'] & [0,1] \arrow[d, "\Phi"] \\
[0,1] \arrow[r, "\widetilde{F}"] & [0,1]
\end{tikzcd}$$

Note: We do not require $\widehat{x}_i = \widetilde{x}_i$ for all i (and $k \in \{0, 1\}$) as is the case in Section 2.2 but treat the more general case needed in Section 2.6.

Proof. Our task is to find a homeomorphism $\Phi : [0,1] \to [0,1]$ with $\widetilde{F} \circ \Phi = \Phi \circ F$. Clearly we will need

$$\Phi(\widehat{x}_i) = \widetilde{x}_i \qquad \forall i \in \{0, ..., k+1\}.$$

Hence we can construct Φ in a piecewise manner for each interval in between two consecutive fixed points of F, $\Phi : [\widehat{x}_i, \widehat{x}_{i+1}] \to [\widetilde{x}_i, \widetilde{x}_{i+1}]$. For simplicity, we may assume $\widehat{x}_i = \widetilde{x}_i = 0$ and $\widehat{x}_{i+1} = \widetilde{x}_{i+1} = 1$ and construct a conjugacy Φ for F and $\widetilde{F}$ where:

- $F(0) = \widetilde{F}(0) = 0$ and $F(1) = \widetilde{F}(1) = 1$.
- W.l.o.g. $F(x) > x$ and $\widetilde{F}(x) > x$ for $x \in [0, 1]$.

Pick $x_0 \in [0, 1]$ and create the following (*forward-backward*) orbits, which in our case are uniquely determined:

$$\{x_t^F\}_{t\in\mathbb{Z}} = \{x_t^F | t \in \mathbb{Z} \text{ such that } x_{t+1} = F(x_t)\}$$
$$\{x_t^{\widetilde{F}}\}_{t\in\mathbb{Z}} = \{x_t^{\widetilde{F}} | t \in \mathbb{Z} \text{ such that } x_{t+1} = \widetilde{F}(x_t)\}$$

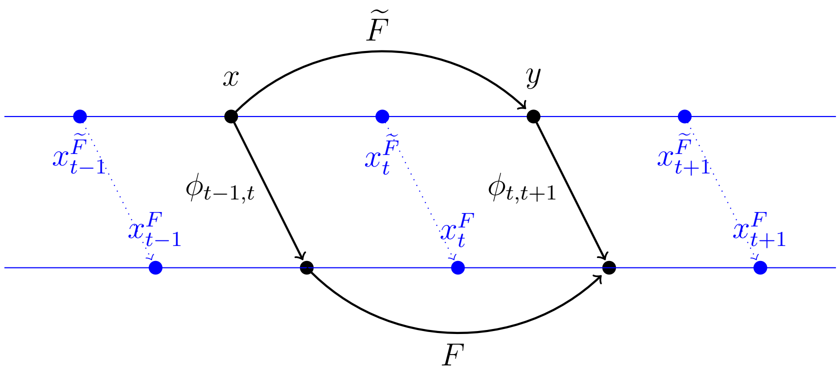
Then $\lim_{t\to\infty} x_t^F = \lim_{t\to\infty} x_t^{\widetilde{F}} = 1$ and $\lim_{t\to-\infty} x_t^F = \lim_{t\to-\infty} x_t^{\widetilde{F}} = 0$. Now define ϕ by $\phi(x_t^{\widetilde{F}}) = x_t^F$ for each $t \in \mathbb{Z}$. Furthermore assume

$$\phi_{0,1} : (x_0^{\widetilde{F}}, x_1^{\widetilde{F}}) \to (x_0^F, x_1^F)$$

to be monotonically increasing and mapping $(x_0^{\widetilde{F}}, x_1^{\widetilde{F}})$ onto (x_0^F, x_1^F). By induction we define $\phi_{t,t+1} : (x_t^{\widetilde{F}}, x_{t+1}^{\widetilde{F}}) \to (x_t^F, x_{t+1}^F)$ for $t \in \mathbb{Z}^+ = \mathbb{N}$ as follows: For each $y \in (x_t^{\widetilde{F}}, x_{t+1}^{\widetilde{F}})$ we find exactly one $x \in (x_{t-1}^{\widetilde{F}}, x_t^{\widetilde{F}})$, such that $y = \widetilde{F}(x)$. Therefore

$$\phi_{t,t+1}\big(\widetilde{F}(x)\big) := F\big(\phi_{t-1,t}(x)\big)$$

maps $(x_t^{\widetilde{F}}, x_{t+1}^{\widetilde{F}})$ onto (x_t^F, x_{t+1}^F) and is monotonically increasing.



For $t \in \mathbb{Z}^-$ proceed analogously. Finally define

$$\Phi(x) = \begin{cases} 0 & x = 0 \\ \phi(x) & x \in \{x_t^{\widetilde{F}}\}_{t \in \mathbb{Z}} \\ 1 & x = 1 \\ \phi_{t,t+1}(x) & x \in \big(x_t^{\widetilde{F}}, x_{t+1}^{\widetilde{F}}\big) \end{cases} .$$

Then $F \circ \Phi = \Phi \circ \widetilde{F}$ and Φ is monotonically increasing. It remains to show that Φ is continuous.
For $x \in \big(x_t^{\widetilde{F}}, x_{t+1}^{\widetilde{F}}\big)$ the case is clear, because every $\phi_{t,t+1}$ has been obtained as a composition of continuous functions. Furthermore, at each node $x = x_t^{\widetilde{F}}$ continuity from the right and the left is induced by $\phi_{0,1}$ being continuous from the right in x_0 and continuous from the left in $x_1^{\widetilde{F}}$. Finally, continuity from the left in $x = 1$ follows from the fact that Φ is increasing and 1 is an upper bound (if $\Phi(x) > 1$ for some $x \in (0, 1)$ we could find a t with $x_t^{\widetilde{F}} > x$ and $\Phi(x_t^{\widetilde{F}}) = x_t^F < 1$, which contradicts monotonicity). By the same argument we find that Φ is continuous from the right in $x = 0$. $\square$

Lemma 5.1.2 (c.f Sections 2.4.2 and 2.6)**.** *For $\zeta \geq 1$ and any of the matrices*

$$(a)\ Z = \begin{pmatrix} \zeta & 1 \\ 1 & 1 \end{pmatrix},\ (b)\ Z = \begin{pmatrix} 1 & 1 \\ 1 & \zeta \end{pmatrix},\ (c)\ Z = \begin{pmatrix} 1 & \zeta \\ \zeta & 1 \end{pmatrix},\ (d)\ Z = \begin{pmatrix} 1 & \zeta \\ \zeta & \zeta \end{pmatrix}$$

define the function $s_\zeta : [0,1] \to [0,1]$ by

$$s_\zeta(x) = x\,\frac{z_{11}x + z_{12}(1-x)}{z_{11}x^2 + x(1-x)(z_{12}+z_{21}) + z_{22}(1-x)^2},$$

(compare equation (2.1) for $J = 1$). Then $\frac{d}{dx}s_\zeta$ is uniformly bounded on every compact interval $[a, 1-a]$, $0 < a < \frac{1}{2}$.

Proof. (a) We set $g(x,\zeta) := \frac{d}{dx}s_\zeta$ and show that

$$g : [a, 1-a] \times [1, \infty) \to \mathbb{R} \qquad 0 < a < \frac{1}{2}$$

is bounded. Obviously g is continuous and nonnegative (s_ζ increasing, c.f. the proof of Proposition 2.1.2). Furthermore, for every $x \in [a, 1-a]$ we have

$$g(x,\zeta) \overset{\zeta\to\infty}{\longrightarrow} 0$$

because g is a quotient of two polynomials where the numerator has lower degree in ζ than the denominator.

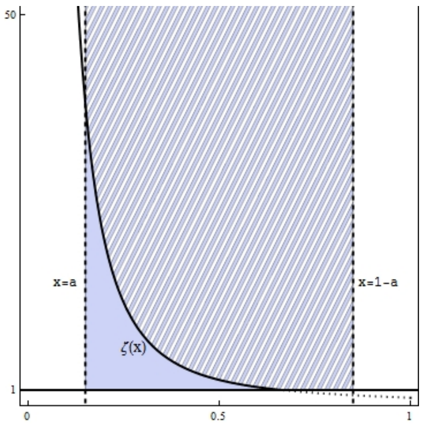
Some computations yield

$$\frac{\partial}{\partial\zeta}g(x,\zeta) = 0 \ \Leftrightarrow\ \zeta = \zeta(x) = \frac{x^3 - 2x^2 + 3x - 2}{x^2(x-2)},$$

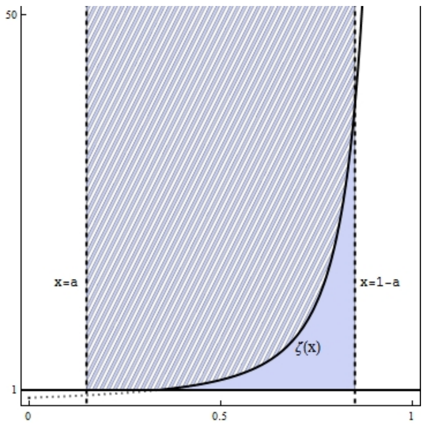
which is bounded for $x \in [a, 1-a]$. Set

$$\overline{\zeta} := \max_{a \leq x \leq 1-a} \zeta(x),$$

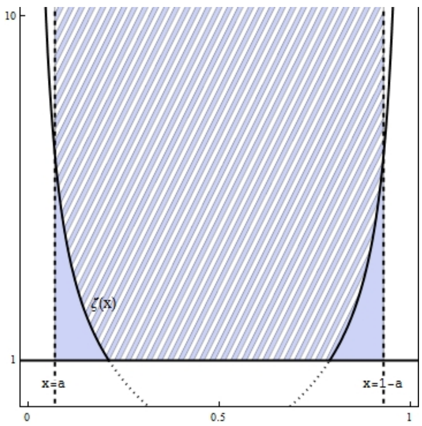
then by the statements above g is decreasing for $\zeta > \overline{\zeta}$ (for any fixed $x \in [a, 1-a]$). Since $[a, 1-a] \times [1, \overline{\zeta}]$ is compact, there must be some $M > 0$ such that $g(x,\zeta) \leq M$ on $[a, 1-a] \times [1, \overline{\zeta}]$ and therefore $g(x,\zeta) \leq M$ on $[a, 1-a] \times [1, \infty)$ as required.



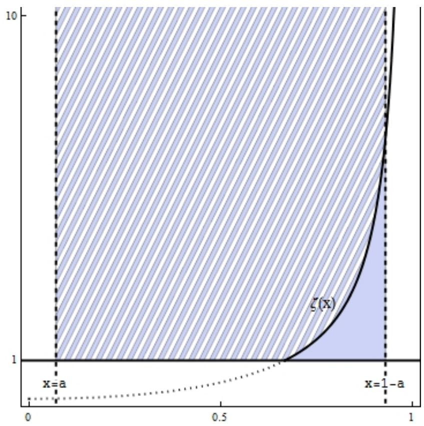
(a)



(b)



(c)



(d)

Figure 5.1: The maximum of $\frac{ds}{dx}$ lies within the pale blue shaded area.

For (b) - (d) the same arguments hold true with

(b) $\zeta(x) = \frac{x-x^2+x^3}{(x-1)^2(x+1)}$ (we may even save ourselves any calculations by noticing that we obtain this case from (a) by $x \mapsto 1-x$),

(c) $\zeta(x) = \frac{1-4x+8x^3-4x^4}{2x(1-3x+4x^2-2x^3)}$ and

(d) $\zeta(x) = \frac{2x^2-x^3}{2-3x+2x^2-x^3}$, where all denominators are > 0 in the region of interest.

$\square$

Lemma 5.1.3 (c.f. Section 3.1.2). *The function*

$$V : \mathrm{int}\Delta \to \mathrm{int}\Delta$$

$$V(x) = \frac{xAx}{x_1x_2x_3}$$

has a unique minimum at $P = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$.

Proof. Although Lagrange's method works just fine we present an approach which is more suitable for manual calculations.
Pick an arbitrary point on the edge of Δ where $x_1 = 0$. This point has the form $(0, s, 1-s)$ for $s \in (0,1)$. The connecting line of this point and the point $x_1 = 1$ is parametrized by $(1-\lambda, \lambda s, \lambda(1-s))$, $\lambda \in (0,1)$. Inserting this into V we obtain

$$V(\lambda, s) = \frac{a\left(1 - 2\lambda + 2\lambda^2(1 - s + s^2)\right) + (b+c)\left(\lambda^2(s - s^2) + \lambda(1-\lambda)\right)}{\lambda^2(1-\lambda)(s-s^2)}.$$

After differenting with respect to s and simplifying the expression we find

$$\frac{\partial V(\lambda, s)}{\partial s} = \frac{(2s-1)\left(a(1 - 2\lambda + 2\lambda^2) + (b+c)\lambda(1-\lambda)\right)}{(1-\lambda)\lambda^2(1-s)^2s^2}.$$

Setting this equal to zero, we see that either $s = \frac{1}{2}$ or $\lambda = \frac{1}{2} \pm \frac{1}{2}\sqrt{\frac{b+c+2a}{b+c-2a}}$. Since the last expression never lies within the interval $(0,1)$, we conclude that any critical point of V must be on the line $(1-\lambda, \frac{1}{2}\lambda, \frac{1}{2}\lambda)$. Thus we investigate $V(\lambda, \frac{1}{2})$:

$$\frac{\partial V\left(\lambda, \frac{1}{2}\right)}{\partial \lambda} = \frac{(3\lambda - 2)\left(2a(2 - 2\lambda + \lambda^2) + (b+c)(2-\lambda)\lambda\right)}{(1-\lambda)^2\lambda^3}$$

From $\frac{\partial}{\partial\lambda}V\left(\lambda, \frac{1}{2}\right) = 0$ we conclude that either $\lambda = 1 \pm \sqrt{\frac{b+c+2a}{b+c-2a}} \notin (0,1)$ or $\lambda = \frac{2}{3}$. Putting this value into the second derivative yields

$$\frac{\partial^2 V\left(\lambda, \frac{1}{2}\right)}{\partial \lambda^2}\Big|_{\lambda=\frac{2}{3}} = \frac{405}{2}a + 81(b+c) > 0.$$

Thus we have a unique minimum on Δ given by $\lambda = \frac{2}{3}$ and $s = \frac{1}{2}$, which corresponds to the point $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$. □

Proposition 5.1.4 (Cannings, 1971; c.f. Section 3.3.2). *The dynamics of the Levene model (1.5) with*

$$W^{(1)} = \begin{pmatrix} 1 & 2 & 2 \\ 2 & 1 & 2 \\ 2 & 2 & 1 \end{pmatrix}, \; W^{(2)} = \begin{pmatrix} 1 & \frac{1}{2} & \frac{1}{2} \\ \frac{1}{2} & 1 & \frac{1}{2} \\ \frac{1}{2} & \frac{1}{2} & 1 \end{pmatrix}, \; n_1 = 1 - n_2 \in \left(\frac{1}{3}, \frac{5}{9}\right)$$

shows a (stable) continuum of fixed points.

Proof. Considering Levene's model, the function $V(p) = \prod_{j=1}^{J}(pW^{(j)}p)^{n_j}$ is a Ljapunov function with $V(p) \leq V(p')$ and equality only at rest points (for a proof of this statement consult, e.g., T. Nagylaki [12], p.145). Thus, looking for equilibria of (1.5) translates into finding extrema of V.
We require $J = 2$ and, for better readability, set $V_j(p) := pW^{(j)}p$. Then we have

$$\frac{\partial V}{\partial p_i} = \frac{\partial}{\partial p_i}\left(V_1^{n_1}V_2^{n_2}\right) = V_1^{n_1-1}V_2^{n_2-1}\left(n_1V_2\frac{\partial V_1}{\partial p_i} + n_2V_1\frac{\partial V_2}{\partial p_i}\right).$$

Suppose that $V_2 = N - KV_1$ for some $N, K > 0$. Substituting this and $n_2 = 1 - n_1$ in the equation above yields

$$\frac{\partial V}{\partial p_i} = V_1^{n_1-1}V_2^{n_2-1}\frac{\partial V_1}{\partial p_i}\left(Nn_1 - KV_1\right).$$

To obtain fixed points we set this expression equal to zero. While $\frac{\partial V_1}{\partial p_i} = 0$ leads to the fixed point $P = \left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$ we already know, $Nn_1 - KV_1 = 0$ for egligible n_1 and V_1 defines a candidate for a curve of equilibria[1]. Now set

$$V_1 = p_1^2 + p_2^2 + p_3^2 + 4(p_1p_2 + p_2p_3 + p_1p_3), \; N = \frac{3}{2}, \; K = \frac{1}{2},$$

then $V_2 = p_1^2+p_2^2+p_3^2+p_1p_2+p_2p_3+p_1p_3$. This corresponds to the proposed configurations of $W^{(1)}$ and $W^{(2)}$ and $Nn_1 - KV_1 = 0$ becomes $3n_1 = V_1$.

[1] To confirm that this surface actually represents the maximum or minimum of V one either has to check the second derivatives or follow the argumentation at the end of this proof.

Easily we calculate that V_1 has its maximum at P with $V(P) = \frac{15}{9}$. Thus we require $n_1 < \frac{5}{9}$ for the curve of equilibria to exist.
Furthermore, if we multiply the left-hand side of $3n_1 = V_1$ by $(p_1+p_2+p_3)^2(= 1)$, we find

$$\underbrace{(1-3n_1)}_{(*)}(p_1^2+p_2^2+p_3^2) + \underbrace{(4-6n_1)}_{(**)}(p_1p_2+p_2p_3+p_1p_3) = 0.$$

In order to find solutions of this equation in Δ it is necessary that $(*)$ and $(**)$ have different signs. This is the case for $n_1 \in \left(\frac{1}{3}, \frac{2}{3}\right)$. Plugging this together with the condition above, we have continua of fixed points for $n_1 \in \left(\frac{1}{3}, \frac{5}{9}\right)$ as required.
To ensure that the curve $Nn_1 - KV_1 = 0$ truly consists of equilibria, we keep in mind that apart from P no other fixed point exists in intΔ and, by formulas (3.5) and (3.9), find out that for $n_1 \in \left(\frac{1}{3}, \frac{5}{9}\right)$ the interior rest point P is a repellor and the system is permanent. Because every orbit must converge somewhere in *int*Δ due to the existence of a Ljapunov function, $Nn_1 - KV_1 = 0$ is a stable equilibrium curve. □

5.2 Part II: Program codes

The program codes presented in this section were written for *Mathematica 6.0*. As this was done by the author of this paper himself to only serve the purposes of his work, there is no claim for technical perfection, elegance or efficiency. In fact, high value has been set on readability and traceability.

Program Code 5.2.1 (Counting fixed points)**.** *The following two programs create a given number of random configurations of (1.2) or (1.5) for $n = 2$ and break it down into the number of fixed points they produce. To do the latter, Sturm's Theorem is applied to achieve reasonable efficiency. Input variables are*

J	...	number of demes
steps	...	number of examples created

For (1.2) the code reads:

```
1  Sturm[J_,steps_] :=
2   Block[{counter,A,nvec,n,f,x,deg,z,sigma,oldcount},
3    Off[Power::"infy"];
4    Off[\infty::"indet"];
5    (*define counters*)
6    For[k=0,k<=2J-1,k++,
7     counter[k]=0];
8    (*compute number of interior fixed points for "step" times*)
9    For[s=1,s<=steps,s++,
10     (*define niche sizes and payoff matrices*)
11     nvec=RandomReal[{0,1},J];
12     For[j=1,j<=J,j++,
13      A[j]=RandomReal[{0,1},{2,2}];
14      n[j]=nvec[[j]]/Sum[nvec[[k]],{k,1,J}]];
15     (*define polynomial, cancel out factors x and (1-x)*)
16     f[x_]=Sum[n[j](A[j][[1,2]]-A[j][[2,2]]+A[j][[1,1]]x-A[j][[1,2]]x-A[j]
           [[2,1]]x+A[j][[2,2]]x) Product[{x,1-x}.A[i].{x,1-x},{i,1,j-1}]
           Product[{x,1-x}.A[i].{x,1-x},{i,j+1,J}]
17         ,{j,1,J}]//Expand;
18     (*algorithm according to Sturm's Theorem*)
19     deg=Exponent[f[x],x];
20     f[0,x_]:=f[x];
21     f[1,x_]:=D[f[z],z]/.{z->x};
22     For[j=2,j<=deg,j++,
23      f[j,x_]=(PolynomialQuotient[f[j-2,z],f[j-1,z],z]/.{z->x})f[j-1,x]-f[j-2,
            x]//Expand//Chop];
24     sigma[x_]:=Count[Table[Sign[f[k,x]]*Sign[f[k-1,x]],{k,1,deg}],-1];
25     (*add 1 to respective counter*)
26     oldcount=counter[sigma[0]-sigma[1]];
27     counter[sigma[0]-sigma[1]]=oldcount+1];
28    Print[Prepend[Table[{k,counter[k]},{k,0,2J-1}],{"#FP","#Examples"}]//
        TableForm]]
```

To adapt this program to model (1.5) simply replace lines 11 *to* 14 *by*

```
nvec=RandomReal[{0, 1}, J];
For[j=1,j<=J,j++,
 B[j]=RandomReal[{0,1},{2,2}];
 A[j]=B[j]+Transpose[B[j]];
 n[j]=nvec[[j]]/Sum[nvec[[k]],{k,1,J}]];
```

Program Code 5.2.2 (Plotting orbits). *Given a set of starting points, this program pictures the corresponding orbits for a panmictic, cyclic game. The following input variables are needed:*

a, *b*, *c*	...	payoff values
starts	...	(a set of) starting points
steps	...	number of generation steps performed

The code reads:

```
CyclicPaths[{a_,b_,c_},starts_ ,steps_]:=
 Block[{A,F,transf,fp,startval,gen},
  (* mapping & transformation on simplex *)
  A=NestList[RotateRight,{a, b, c},2];
  F[x_]:=x*A.x/x.A.x;
  transf[{x_,y_,z_}]:={y+z/2,Sqrt[3]z/2};
  (* create set of fixed points *)
  If[0<a-b<2a-b-c||2a-b-c<a-b<0,
   fp=Join[{{1/3,1/3,1/3},{1,0,0},{0,1,0},{0,0,1}},NestList[RotateRight,{(a-
       b)/(2a-b-c),1-(a-b)/(2a-b-c),0},2]],
   fp={{1/3,1/3,1/3},{1,0,0},{0,1,0},{0,0,1}}];
  (* generate orbits *)
  startval=Flatten[Table[NestList[RotateRight,starts[[k]],2],{k,1,Length[
       starts]}],1];
  Table[gen[g]=Table[Nest[F,startval[[j]],g],{j,1,Length[startval]}],{g,0,
       steps}];
  (* graphics *)
  Show[{
     RegionPlot[Sqrt[3]a1-a2<0,{a1,0,.5},{a2,0,1},DisplayFunction->Identity,
          PlotStyle->White,BoundaryStyle->None],
     RegionPlot[Sqrt[3]a1+a2>Sqrt[3],{a1,.5,1},{a2,0,1},DisplayFunction->
          Identity,PlotStyle->White,BoundaryStyle->None],
     RegionPlot[a2<0,{a1,0,1},{a2,-.2,1},DisplayFunction->Identity,PlotStyle
          ->White,BoundaryStyle->None],
     ListPlot[{{0,0},{1,0},{.5,Sqrt[3]/2},{0,0}},Joined->True,PlotStyle->{
          Black,Thickness[.005]}],
     Table[ListPlot[Table[transf[x]/.x->gen[g][[j]],{j,1,Length[startval]}],
          PlotStyle->{RGBColor[(g/steps)^(1/2),0,1-(g/steps)^(1/2)]}],{g,0,
          steps}],
     ListPlot[Table[transf[x]/.x->fp[[k]],{k,1,Length[fp]}],Joined->False,
          PlotStyle->{Black,PointSize[Large]}]
     },
   AspectRatio->Automatic,Frame->False,PlotRange->{{0,1},{0,1}}]]
```

Program Code 5.2.3 (Animated simulation)**.** *Specify the following data*

A, B	...	payoff matrices
$n1$, $n2$	...	niche proportions (adding up to 1)
d	...	density of grid put upon Δ
timesteps	...	number of timesteps performed
genstep	...	number of generations passing in one timestep
speed	...	speed of the animation (default value is 1).

Then the following lines will create a sequence of pictures consecutively showing the initial values (green) with their succeeding points (red).

```
Simul[A_,B_,n1_,n2_,d_,timesteps_,genstep_,speed_]:=
 Block[
  {f,pregrid,grid,plotgrid,imggrid,plotimggrid,transformation,graphics},
  f[x_]:=x*(n1*A.x/x.A.x+n2*B.x/x.B.x);
  transformation[{a_,b_,c_}]:={b+c/2,Sqrt[3]c/2};
  pregrid=Flatten[Table[{k/d,(n-k)/d,(d-n)/d},{k,0,d},{n,k,d}],1];
  For[z=1,z<timesteps+1,z++,
   (* initial points *)
   grid=pregrid;
   plotgrid=Table[transformation[grid[[j]]],{j,1,Length[grid]}];
   (* points after applying f *)
   imggrid=Table[Nest[f,grid[[j]],genstep],{j,1,Length[grid]}];
   plotimggrid=Table[transformation[imggrid[[j]]],{j,1,Length[grid]}];
   (* create graphics *)
   graphics[z]=Show[{
      RegionPlot[Sqrt[3]a1-a2<0,{a1,0,.5},{a2,0,1},DisplayFunction->Identity
         ,PlotStyle->White,BoundaryStyle->None],
      RegionPlot[Sqrt[3]a1+a2>Sqrt[3],{a1,.5,1},{a2,0,1},DisplayFunction->
         Identity,PlotStyle->White,BoundaryStyle->None],
      RegionPlot[a2<0,{a1,0,1},{a2,-.2,1},DisplayFunction->Identity,
         PlotStyle->White,BoundaryStyle->None],
      ListPlot[{{0,0},{1,0},{.5,Sqrt[3]/2},{0, 0}},Joined->True,PlotStyle->{
         Black,Thickness[.005]}],
      Table[ListPlot[{plotgrid[[i]],plotimggrid[[i]]},Joined->True,PlotStyle
         ->{Green}],{i,1,Length[grid]}],
      ListPlot[plotgrid,Joined->False,PlotStyle->{Green}],
      ListPlot[plotimggrid,Joined->False,PlotStyle->{Red}]
      },
     AspectRatio->Automatic,Frame->False,PlotRange->{{0,1},{0,1}}];
   pregrid=imggrid];
  ListAnimate[Table[graphics[x],{x,1,timesteps}],AnimationRate->speed,
      AnimationRepetitions->1]]
```

For instance in the case of closed orbits it might be helpful to indicate initial and end points by arrows, which can be done by replacing lines 15 *to* 25 *by*

```
graphics[z]=Show[{
        RegionPlot[Sqrt[3]a1-a2<0,{a1,0,.5},{a2,0,1},DisplayFunction->Identity
            ,PlotStyle->White,BoundaryStyle->None],
        RegionPlot[Sqrt[3]a1+a2>Sqrt[3],{a1,.5,1},{a2,0,1},DisplayFunction->
            Identity,PlotStyle->White,BoundaryStyle->None],
        RegionPlot[a2<0,{a1,0,1},{a2,-.2,1},DisplayFunction->Identity,
            PlotStyle->White,BoundaryStyle->None],
        ListPlot[{{0,0},{1,0},{.5,Sqrt[3]/2},{0,0}},Joined->True,PlotStyle->{
            Black,Thickness[.005]}],
        Graphics[Table[{Arrowheads[Small],Arrow[{plotgrid[[i]],plotimggrid[[i
            ]]}]},{i,1,Length[grid]}]],
        ListPlot[plotgrid,Joined->False,PlotStyle->{Green}],
        ListPlot[plotimggrid,Joined->False,PlotStyle->{Red}]
        },
      AspectRatio->Automatic,Frame->False,PlotRange->{{0,1},{0,1}}];
  pregrid=imggrid];
```

Bibliography

[1] R. Bürger. *Einführung in die mathematische Populationsgenetik*. Lecture notes, 2008.

[2] C. Cannings. Natural selection at a multiallelic autosomal locus with multiple niches. *Journal of Genetics*, 60(3):255–259, 1971.

[3] A.W.F. Edwards. *Foundations of Mathematical Genetics*. Cambridge University Press, 1977.

[4] A. Gaunersdorfer. Time averages for heteroclinic attractors. *SIAM Journal on Applied Mathematics*, 52(5):1476–1489, 1992.

[5] J. Hofbauer. A difference equation model for the hypercycle. *SIAM Journal on Applied Mathematics*, 44(4):762–772, 1984.

[6] J. Hofbauer. *Biomathematik*. Lecture notes, 2007.

[7] J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, 1998.

[8] J. Hofbauer and J.W.H. So. Uniform persistence and repellors for maps. *Proceedings of the American Mathematical Society*, 107(4):1137–1142, 1989.

[9] S. Karlin. Gene frequency patterns in the Levene subdivided population model. *Theoretical Population Biology*, 11(3):356, 1977.

[10] H. Levene. Genetic equilibrium when more than one ecological niche is available. *The American Naturalist*, 87(836):331, 1953.

[11] M.P. Mistelbauer. Evolution in selection-migration models with a focus on the Levene model. Master's thesis, University of Vienna, 2008.

[12] T. Nagylaki. *Introduction to Theoretical Population Genetics*. Springer, 1992.

[13] S. Novak. The number of equilibria in the diallelic Levene model with multiple demes. *submitted*, 2010.

Curriculum Vitae

Personal Data

Name:	Sebastian Novak
Date of Birth:	13 November, 1984
Place of Birth:	Tulln a.d. Donau, Austria
Citizenship:	Austria

Education

10/1995-06/2003	Bundesgymnasium Tulln a.d. Donau
10/2003-05/2004	Military Service at Fliegerhorst Brumowski, ET X/03
10/2004-06/2009	Instrumental Studies Accordion at the Konservatorium Wien Privatuniversität (BA)
10/2004-07/2010	Diploma Studies in Mathematics at the University of Vienna, Austria