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Evolution in Selection-Migration Models with a Focus on the Levene Model

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CHAPTER 0

INTRODUCTION

The present diploma thesis is written in the field of mathematical population genetics and examines the evolution of a population under the joint action of selection and migration. The focus is laid on origin-independent migration as stated by the Levene model. The content of the six chapters is briefly described below. The literature consulted is quoted throughout the text.

We begin with summarizing some biological basics in Chapter 1 and define the properties assigned to the population which is underlying our models.

In Chapter 2 we introduce the general selection-migration model which will be the object of investigation in Chapters 3 and 4. After formulating the basic selection-migration model, we distinguish between soft and hard selection, and observe how the dynamics change in the special case of no dominance.

We continue the analysis of the basic selection-migration model in Chapter 3 and present some general results. These concern protected polymorphisms in the diallelic case, a condition for the number of alleles that can be maintained at equilibrium if there is no dominance, the fixation of an allele, weak and strong migration, as well as uniform selection.

Applying some of the results treated in Chapter 3, we give examples and consider special cases in Chapter 4. They illustrate and support the understanding of the theory.

The main part of this work is devoted to the Levene model, a special case of the general selection-migration model. It is studied in Chapter 5 which is subdivided into four sections. The approach to investigate the Levene model is similar to that of the general selection-migration model: At first, in Section 5.1, we state its dynamics, formulate it for soft and hard selection, and derive its dynamics if there is no dominance. In Section 5.2 we present some general results for the Levene model about the existence of a unique, stable equilibrium, the equilibrium if there is no dominance, arbitrarily many alleles at equilibrium, as well as results about loss and fixation of an allele. The Levene model with two alleles is studied in detail in Section 5.3, including analyses about the number of possible equilibria, protected polymorphisms, and the maximum number of polymorphic equilibrium points given diverse selection regimes. In the last section about the Levene model, Section 5.4, we perform some analytical and numerical calculations for diverse combinations of alleles, niches and dominance patterns in order to determine the volume of the parameter space at which a protected polymorphism occurs, or at which a certain number of alleles is maintained in the population.

The work concludes with Chapter 6 in which we summarize and discuss the main aspects of this diploma thesis.

Enclosed are the Appendix with PSTricks and Octave source codes, the Bibliography with a complete list of references consulted to write this thesis, a summary in german, and my Curriculum Vitae.

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CHAPTER 1

POPULATION GENETIC TERMINOLOGY

In this chapter we give a brief overview of elementary population genetics and specify the basic assumptions that will be made in this thesis.

We consider a subdivided population, which means that the population consists of subpopulations which occupy a finite number of distinct ecological niches. Individuals are exchanged between these subpopulations. Every niche has its own selection scheme acting on the subpopulation living there. In this work, only discrete-space and discrete-time models will be considered. The generations are therefore nonoverlapping, and every point in time represents the beginning of the next generation which replaces the preceding one. The discreteness of space is attained by assuming that we have a finite number of separate niches, thus, an individual in one deme cannot be in another one at the same time. Speaking in this way also the niches are nonoverlapping. But in what kind of terms can the evolution of the population be expressed?

We consider a gene which, roughly, is a specific region of the DNA that codes for a polypeptide chain. The region on the DNA, where the gene is situated, is the locus, and a particular sequence there is an allele. At a specific locus we may have two, three or more different expressions of a gene in the population, so we are speaking of a diallelic, triallelic or multiallelic locus.

If we are interested in how the population structure changes genetically, we observe a locus and study how the allelic proportions in the population evolve in time. Therefore, we may obtain information on which alleles get fixed, which get lost, or if there is a polymorphic equilibrium.

Since in population genetics, “gen” is sometimes refered to as “allele”, the proportion of a particular allele in the population might as well be called gene frequency rather than allelic frequency, as it is called throughout this work.

Depending on the species, the number of chromosomes differs. A chromosome is contained in the nucleus of a cell and is a single thread-like molecule of DNA, along which genes are arranged. In haploid populations (bacteria, many algae, mosses and fungi) the set of chromosomes of each individual is simple and reproduction takes place asexually by duplication. In diploid organisms (most higher plants and animals) the chromosomes usually form homologous pairs. Sexual reproduction involves recombination, i.e., during meosis the chromosomes separate, crossing over between two homologous chromosomes may occur, and subsequent uniting during fertilization forms a diploid zygote from which the offspring develops ([10], p. 1-4).

The process of recombination is a substantial distinction between sexual reproduction and asexual. The zygote has maternal alleles in one set of loci and paternal ones at the complementary. So there is the potential to combine favorable alleles of different ancestors and break up deleterious allele combinations.

If we take into account a single locus, the particular allelic composition of an individual is the genotype. The observable expression of the genotype is called the phenotype. A single locus of a diploid organism can be homozygous (A_iA_i, A_jA_j) or heterozygous (A_iA_j) depending if the two genes are of the same allelic type or not, where $i, j \in J$ and J denotes the number of alleles present at the locus.

A population is said to be monoecious if every individual has both male and female sexual organs and, therefore, can be described by one set of genotypic proportions. Otherwise, it is dioecious.

Furthermore, we suppose that there are two alleles, A_1 and A_2. An allele is called dominant to the other if the expressed phenotypes of A_1A_1 and A_1A_2 are the same. Recessive alleles are only expressed in homozygotes. The genetic composition of a population in deterministic models is described by genotypic or allelic frequencies. The dynamics are governed by a few elementary genetic principles such as Mendelian inheritance and recombination, and evolutionary forces such as mutation, selection and migration. In this work we always assume that the population and every subpopulation is sufficiently large to neglect random genetic drift. Thus, the probabilistic variation of gene frequencies in a finite population due to random sampling of genes is ignored ([2], p. 1-5).

The mating system has also a very big influence on the genetic evolution of a population. In this work we always assume random mating, i.e., mating is independent of genotype and ancestry. It is the simplest possible situation and seems to occur frequently in nature. Consequently, the law of Hardy-Weinberg states that random mating conserves allele frequencies, or in other words the genetic variability, and after one generation also genotypic frequencies due to random combination of the genes at one locus ([14], p. 119-121).

Mutations are changes of the genetic material and they are the ultimate source of genetic variability. However, in this work we will asume that the effect of selection is much stronger than that of mutation, so it affects only the dynamics of rare alleles out of the existing ones and is therefore not taken into account.

Selection takes place when different genotypes vary in their probability of surviving to adulthood (viability), their mating success, or in their average number of produced offspring (fertility). They therefore differ in their fitness, which means that they have a different number of progeny that they contribute to the next generation. Unless the population is in equilibrium, selection will change the allelic frequencies as well as the genotypic frequencies. In a subdivided population we distinguish between the local selection regimes that act in each subpopulation, and the global selection pattern which is the collection of all local selection functions ([8], p. 222-225).

Most natural populations are subdivided and mate at random only locally. Therefore, it is important to consider the effect of geographically structured populations on genetic variation and under which conditions genetic variation is independent of the geographical distribution. We will further assume that only adult individuals migrate and that they migrate independently of their genotype.

The assumptions on the population are the following and might be modified or adjusted if necessary:

- generations are discrete and nonoverlapping
- the population is subdivided into K panmictic colonies
- a single locus is considered with J alleles A_i, $i = 1, \dots, J$
- the population is monoecious and diploid
- selection acts solely through viability differences
- fertilities are constant
- adult migrants are exchanged
- migration is independent of genotype
- reproduction takes place by random mating in each niche
- mutation and random genetic drift are neglected

CHAPTER 2

THE BASIC SELECTION-MIGRATION MODEL

We formulate the general selection-migration model according to Nagylaki ([10], p. 132-135, [13], p. 22-23) and, therefore, we consider a population that fulfills all the assumptions listed at the end of Chapter 1. Designating the sets of alleles and demes by $\mathcal{J}$ and $\mathcal{K}$, respectively, we have

$$i \in \mathcal{J} = \{1, 2, \dots, J\}, \qquad k \in \mathcal{K} = \{1, 2, \dots, K\}. \tag{2.1}$$

For every $i \in \mathcal{J}$ and $k \in \mathcal{K}$ we also define

$$\mathcal{J}_i = \{j \in \mathcal{J} : j \neq i\}, \qquad \mathcal{K}_k = \{l \in \mathcal{K} : l \neq k\}. \tag{2.2}$$

The life cycle of the population consists of 4 stages: selection, migraton, population regulation and reproduction.

Let c_k, c_k^*, c_k^{**}, and $c_k^{'}$ denote the proportion of individuals in deme k before selection (zygotes), after selection, after migration, and after regulation, respectively. The frequency of the allele A_i in niche k in generation t $(= 0, 1, 2, \dots)$ is $p_{i,k}(t)$ and $p_{i,k}^*$, $p_{i,k}^{**}$, and $p_{i,k}^{'}$ correspond to these stages. Therefore, we can represent the life cycle ([10], p. 133) as shown in Table 2.1. Due to random mating in each niche, the subpopulations return to Hardy-Weinberg proportions during reproduction.

Zygote	$\longrightarrow$	Adult	$\longrightarrow$	Adult	$\longrightarrow$	Adult	$\longrightarrow$	Zygote
	Selection		Migration		Pop. Reg.		Reproduction	
$c_k p_{i,k}$	$\longrightarrow$	$c_k^* p_{i,k}^*$	$\longrightarrow$	$c_k^{**} p_{i,k}^{'}$	$\longrightarrow$	$c_k^{'} p_{i,k}^{'}$	$\longrightarrow$	$c_i^{'} p_{i,k}^{'}$

Table 2.1: Life cycle

For every $k \in \mathcal{K}$ the nonnegative variables $p_{i,k}$ and c_k satisfy

$$\sum_i p_{i,k} = 1, \qquad \sum_k c_k = 1, \tag{2.3}$$

respectively. The simplex is denoted by

$$\Delta_J = \left\{ z \in \mathbb{R}^J : z_i \geq 0, \forall i \in \mathcal{J}, \sum_{j=1}^{J} z_j = 1 \right\}. \tag{2.4}$$

We write $\Delta_J^K = (\Delta_J)^K$ and define the following column vectors

$$\begin{aligned} p_i &= (p_{i,1}, \dots, p_{i,K})^T \in \mathbb{R}^K, \\ p^{(k)} &= (p_{1,k}, \dots, p_{J,k})^T \in \Delta_J, \\ p &= (p^{(1)}; \dots; p^{(K)})^T \in \Delta_J^K, \end{aligned} \tag{2.5}$$

where p_i, $p^{(k)}$, and p denote the frequencies of A_i in each niche, the gene frequencies in deme k, and all gene frequencies, respectively.

We designate the viability of an A_iA_j individual in deme k by $w_{ij,k}$. The mean fitness of individuals that carry A_i and of all individuals in deme k then is

$$w_{i,k}(p^{(k)}) = \sum_j w_{ij,k} p_{j,k} \tag{2.6}$$

and

$$\bar{w}_k(p^{(k)}) = \sum_i w_{i,k} p_{i,k} = \sum_{i,j} w_{ij,k} p_{i,k} p_{j,k}, \tag{2.7}$$

respectively. For every $i, j \in \mathcal{J}$ and $k \in \mathcal{K}$ we have $w_{ij,k} = w_{ji,k}$ because in general, the genotypes A_iA_j and A_jA_i cannot be distinguished. The frequency of A_i after selection in deme k is given by

$$p^*_{i,k} = p_{i,k} \frac{w_{i,k}}{\bar{w}_k}. \tag{2.8}$$

To describe migration among colonies we define the forward and backward migration matrices $\tilde{M}$ and M. Their elements $\tilde{m}_{kl}$ and m_{kl} are characterized as follows:

- $\tilde{m}_{kl}$ denotes the prospective conditional probability that an adult individuum in niche k migrates to niche l.
- m_{kl} designates the retrospecive conditional probability that an individual in deme k after migration came from deme l.

The gene frequencies in the next generation are given by

$$p'_{i,k} = \sum_l m_{kl} p^*_{i,l}, \tag{2.9}$$

where $p^*_{i,l}$ is the allelic frequency after selection given by (2.8). Equations (2.8) and (2.9) fully describe the dynamics of the basic selection-migration model ([10], p. 132-135).

Obviously, every individuum must come from some niche and migrate to some niche, therefore we have

$$\sum_l m_{kl} = 1, \qquad \sum_k \tilde{m}_{lk} = 1, \tag{2.10}$$

with $m_{kl} \geq 0$ and $\tilde{m}_{lk} \geq 0$ for every $k, l \in \mathcal{K}$. Thus, the $K \times K$ migration matrices $M = (m_{kl})$ and $\tilde{M} = (\tilde{m}_{lk})$ are stochastic.

Since no individuals can get lost during migration we obtain the forward and backward migration equation

$$c_k^{**} = \sum_l c_l^* \tilde{m}_{lk} \tag{2.11}$$

and

$$c_l^* = \sum_k c_k^{**} m_{kl}, \tag{2.12}$$

respectively. The joint probability that an adult individuum that is in niche l and migrates to niche k yields

$$c_l^* \tilde{m}_{lk} = c_k^{**} m_{kl}. \tag{2.13}$$

Inserting (2.11) in (2.13) gives

$$m_{kl} = \frac{c_l^* \tilde{m}_{lk}}{c_k^{**}} = \frac{c_l^* \tilde{m}_{lk}}{\sum_n c_n^* \tilde{m}_{nk}}. \tag{2.14}$$

The above relation enables us to calculate the backward migration matrix from the forward migration matrix given the deme sizes after selection and also viceversa. If a migration pattern does not change niche proportions ($c_i^{**} = c_i^*$ for every $i \in \mathcal{J}$) we shall call it conservative.

With (2.8) and (2.9) the basic selection-migration model is completely determined if m_{kl} is known. But if, instead of M, we are given the distribution of emigrants from each deme, thus $\tilde{M}$, we must compute M from (2.14) to obtain a complete description of the model.

Therefore, we need an Ansatz for $c^* = (c_1^*, \ldots, c_K^*)^T \in \mathrm{int}\Delta_K$ in terms of $c = (c_1, \ldots, c_K)^T \in \mathrm{int}\Delta_K$, which is in accordance with the nature of selection. Most analysis have been devoted to two possible extreme assumptions: soft or hard selection ([11], p. 299).

2.1 Soft Selection

During selection the deme sizes remain the same relatively to the others, which means that the population is regulated within each deme such that

$$c^* = c. \tag{2.15}$$

It follows from (2.14) that in this case M is constant and our model is complete. Soft selection is often assumed when selection takes place only locally, as it can be observed in plant populations. In this paper we are going to investigate mainly soft selection.

2.2 Hard Selection

If the total population size is controlled, it is better to suppose that the deme sizes after selection are depending on the ratio of their fitness $\bar{w}_k$ to that of the entire population $\bar{w}$. The fraction of adults is proportional to the mean fitness in each niche

$$c_k^* = c_k \frac{\bar{w}_k}{\bar{w}}, \tag{2.16}$$

where

$$\bar{w} = \sum_{l=1}^{K} c_l \bar{w}_l. \tag{2.17}$$

Hard selection describes global selection as it can be assumed for some animals.

2.3 No Dominance

The special case without dominance ([11], p. 299) is of particular biological interest and in the following chapters we are often going to assume no dominance. It means that there exist constants $v_{i,k}$ such that $w_{ij,k}$ can be written as

$$w_{ij,k} = v_{i,k} + v_{j,k} \tag{2.18}$$

for every $i, j \in \mathcal{J}$ and $k \in \mathcal{K}$. Thus, the genotype A_iA_j has additive fitness, since $v_{i,k}$ describes the fitness of allele A_i in niche k. Substituting (2.18) in (2.6) and (2.7) yields

$$w_{i,k} = v_{i,k} + \bar{v}_k, \qquad \bar{w}_k = 2\bar{v}_k, \tag{2.19}$$

where

$$\bar{v}_k(p^{(k)}) = \sum_i v_{i,k} p_{i,k}. \tag{2.20}$$

We point out that $\bar{v}_k(p^{(k)})$ is linear, whereas $\bar{w}_k$ is quadratic. Therefore, the selection-migration dynamics (2.9) become

$$p_{i,k}^{'} = \sum_l m_{kl} p_{i,l} \frac{(v_{i,l} + \bar{v}_l)}{2\bar{v}_l}. \tag{2.21}$$

CHAPTER 3

GENERAL RESULTS

In this chapter we study some general results of the selection-migration model, but first we explain some concepts. We say that the allelic frequencies are at equilibrium if they remain constant after finitly many generations, thus, if $p_{i,k}^{'} = p_{i,k}$ for every $k \in \mathcal{K}$.

An equilibrium is said to be stable if the population remains within an arbitrarily small, preassigned distance of the equilibrium, provided it starts sufficiently close to it. If the equilibrium is stable and an attractor, which means that a population that starts sufficiently close to the equilibrium converges to it, it is called asymptotically stable.

If every trajectory on the simplex Δ_{J}^{K} is converging to the equilibrium, it is globally stable. For a locally stable equilibrium only the trajectories which are sufficiently close, converge to it. If an equilibrium is not stable, thus, if at least one trajectory is diverging of the equilibrium, we say that it is unstable ([5], p. 187-188).

An equilibrium is called a fixation state if in every niche an allele is fixed, thus, if for every $k \in \mathcal{K}$ there exists an $i \in \mathcal{J}$, such that $p_{i,k} = 1$. Every equilibrium at which no allele is fixed in every niche, is polymorphic. An equilibrium is said to be fully polymorphic or internal, if every allele is present in each niche, thus, if $p_{i,k} > 0$ for every $i \in \mathcal{J}$ and every $k \in \mathcal{K}$.

3.1 Protected Polymorphism in the Diallelic Case

Let us suppose a diallelic locus with the two alleles A and a. Clearly, it suffices to examine the gene frequency of one allele in every deme k, since $p_{2,k} = 1 - p_{1,k}$. Let therefore $p_k = p_{1,k}$ be the gene frequency of allele A in deme k. We seek to find sufficient conditions for the existence of a protected polymorphism in the diallelic case. The multiallelic case is far more difficult and we cannot derive useful protection conditions. Allele A is protected if it cannot be lost, which means that $p = (p_1, \ldots, p_k) = (0, \ldots, 0)$ is unstable and at least one of the p_k is increasing if p is getting very small. We are speaking of a protected polymorphism, if every allele is protected. In our case of a diallelic locus this means that the trivial equilibria $p = (0, \ldots, 0)$ at which A is lost and

a is fixed, and $p = (1, \dots, 1)$ at which a is lost and A is fixed, are unstable. Further, it guarantees that both alleles will increase in frequency when rare. Thus, none of the two alleles can get fixed or lost. A protected polymorphism does not say anything about the existence of an internal equilibrium (cf. [3]).

We define the fitness values for the diallelic case as they are shown in Table 3.1, where we suppose that u_k and v_k are constant and both > 0 for every $k \in \mathcal{K}$.

Genotypes	AA	Aa	aa
Fitness Values	$w_{11,k}$	$w_{12,k}$	$w_{22,k}$
Relative Fitness Values	$u_k = \frac{w_{11,k}}{w_{12,k}}$	1	$v_k = \frac{w_{22,k}}{w_{12,k}}$

Table 3.1: Relative fitness values for two alleles

For $p = (0, \dots, 0)$ to be unstable, the absolute value of at least one eigenvalue of the Jacobian matrix needs to exceed unity ([4], p. 256). In order to obtain a sufficient condition for the protection of A, we need to linearize the general selection-migration dynamics described by (2.9) and (2.8). If we assume that we know p_i^* for every $i \in \mathcal{J}$, (2.9) is already linear and it suffices to linearize (2.8) near $p = (0, \dots, 0)$.

The Jacobian matrix of (2.8) at $p = (0, \dots, 0)$ is the diagonal matrix D, where $d_{kk} = \frac{1}{v_k}$. By setting $Q = MD$, we obtain the Jacobian matrix of the entire selection-migration dynamics at $p = (0, \dots, 0)$. Thus, the linearized recursion equation is

$$p' = Qp \tag{3.1}$$

with

$$Q = (q_{lk}), \qquad q_{lk} = \frac{m_{lk}}{v_k}. \tag{3.2}$$

A substantial Theorem derived from ([10], p. 136-137) concerning the protection of an allele in the diallelic case, is the following:

Theorem 3.1. *Suppose M is irreducible. Then there exists a real, positive, maximal eigenvalue λ_0 of Q and a corresponding strict positive eigenvector. Thus, A is protected if $\lambda_0 > 1$ and A is not protected if $\lambda_0 < 1$. Moreover, the maximal eigenvalue λ_0 satisfies the inequality*

$$\min_l \sum_k q_{lk} \geq \lambda_0 \geq \max_l \sum_k q_{lk} \tag{3.3}$$

with equality if and only if all row sums are the same.

Proof. We suppose that M is irreducible, thus, the n-th generation descendant of an individual from any subsystem has a positive probability to be in any other niche. If M is irreducible, so is Q and since Q is clearly nonnegative, Frobenius' Theorem tells us that there exists a real positive eigenvalue λ_0 of Q with $|\lambda| \geq \lambda_0$ for all other eigenvalues. To λ_0, the so-called maximal eigenvalue of Q corresponds a strict positive eigenvector. One can prove that the positive maximal eigenvector of Q is orthogonal to every vector in the eigenspace complementary to the maximal (right) eigenvector. Therefore there are no nonnegative vectors in that space and the results follow. ☐

In the diallelic case, a necessary condition for a protected polymorphism is that selection changes direction at least once, which means that A is favoured in some demes and a elsewhere, and that selection is sufficiently strong relative to migration ([14], p. 124).

We shall say that local directed selection is in force in deme k if either $u_k \leq 1 \leq v_k$ or $u_k \geq 1 \geq v_k$. We have overdominance in niche k if $\max(u_k, v_k) < 1$, and underdominance if $\min(u_k, v_k) > 1$. A global selection regime is simply the collection of all the local selection functions. In the case of two alleles and viability selection as given by (2.8) it suffices to take into account the fitness parameter array $(u_1, v_1), (u_2, v_2), \dots, (u_K, v_K)$. We distinguish four global selection regimes: a mosaic pattern of directional selection, overdominance in every niche, underdominance thoughout the range and a mixed underdominant-overdominant regime ([7], p. 358-359).

We now return to the multiallelic case and investigate the behaviour of (2.9) in the absence of dominance.

3.2 Equilibria If There Is No Dominance

Before we can establish the main result of this subsection, which was stated by Nagylaki and Lou ([11], p. 300), we need to define what it means when a property holds generically.

Definition 3.2. *A property is called generic if it holds for almost all fitnesses, migration matrices, and deme proportions, i.e. for an open, dense set of full measure.*

Theorem 3.3. *Without dominance, the number of demes is a generic upper bound on the number of alleles present at equilibrium.*

This result is equally valid for hard selection and, as we will prove in Subsection 5.2.2, also applies to the Levene model. Since (2.9) need not converge, Theorem 3.3 does not imply loss of an allele when $J > K$.

How this Theorem corresponds with intuition is not quite clear. One could imagine that in order for an internal equilibrium to exist, each allele must be the fittest in some deme, but this is not the case.

By modifying the proof of Theorem 3.3 slightly, one can establish the Theorem for multiplicative fitnesses: So there exist constants $v_{i,k}$ which represent the fitness of allele A_i in niche k, such that

$$w_{ij,k} = v_{i,k} v_{j,k} \tag{3.4}$$

for every $i, j \in \mathcal{J}$ and every $k \in \mathcal{K}$. It follows from (2.6), (2.7) and (3.4) that

$$w_{i,k} = v_{i,k} \bar{v}_k, \qquad \bar{w}_k = \bar{v}_k^2. \tag{3.5}$$

If we assume intermediate dominance, that is

$$\min(w_{ii,k}, w_{jj,k}) \leq w_{ij,k} \leq \max(w_{ii,k}, w_{jj,k}) \tag{3.6}$$

for every $i, j \in \mathcal{J}$ and every $k \in \mathcal{K}$, and posit sufficiently weak migration, then the Theorem holds under multiplicative fitness. However, if migration is sufficiently strong Theorem 3.3 does not extent to 3.6 ([14], p. 125).

3.3 Fixation of an Allele

We say that an allele is fixed in the population if it is fixed in every niche, thus, all the other alleles go extinct. The following proposition from Nagylaki and Lou ([13], p. 24) establishes a fixation condition for allele A_1 in the gerneral selection migration model.

Proposition 3.4. *Suppose that (2.9) holds, M is irreducible and that*

$$w_{1i,k} + w_{1j,k} \geq 2w_{ij,k} \tag{3.7}$$

for every $i, j \in \mathcal{J}$ and for every $k \in \mathcal{K}$. Further we assume that $p_1(0) > 0$ and $w_{11,k} > w_{1i,k}$ or $w_{1i,k} > w_{ii,k}$ for every $i \in \mathcal{J}_1$. Then $p_1(t) \longrightarrow (1, \dots, 1)^T$ as $t \longrightarrow \infty$.

Due to the irreducibility of M it suffices to assume initial presence of A_1 in some deme, i.e. $p_{1,k}(0) > 0$ for some $k \in \mathcal{K}$. Setting $j = 1$ and $j = i$ in (3.7) leads, respectively, to the two strict inequalities in the proposition. We see that A_1 is neither underdominant nor overdominant with any other allele in any deme. Since Proposition 3.4 holds under arbitrary migration, it also applies also to the Levene model ([14], p. 125).

3.4 Weak Migration

In this section we investigate the behaviour of the general selecton-migration model (2.9) under weak migration. Since, without migration the map (2.9) reduces to the pure-selection mapping in a subdivided population

$$p'_{i,k} = p_{i,k} \frac{w_{i,k}(p^{(k)})}{\bar{w}_k(p^{(k)})} \tag{3.8}$$

for every $i \in \mathcal{J}$ and every $k \in \mathcal{K}$, we know that the gene frequency in (3.8) always converges ([2], p. 17-20). We now study what happens if we introduce weak gene flow between the niches in the pure-selection mapping (3.8). We would want the features of the model to qualitatively remain the same under small perturbations of the migration parameters. So in the neighborhood of each locally asymptocially stable equilibrium under pure selection, there should exist exactly one locally asymptotically stable equilibrium under weak migration. Indeed, Theorem 3.7 shall tell us, besides other results, exactly that.

Migration is considered to be weak if the backward migration matrix is sufficiently close to the $K \times K$ identy matrix I, thus $1 - m_{kk} > 0$ for every $k \in \mathcal{K}$, but $M \neq I$. So for fixed fitnesses $w_{ij,k}$, we can set the backward migration rate

$$m_{kl} = \delta_{kl} + \varepsilon \mu_{kl} \tag{3.9}$$

for every $k, l \in \mathcal{K}$ where δ_{kl} represents the Kronecker delta, so that $\delta_{kk} = 1$ and $\delta_{kl} = 0$ if $k \neq l$ and let $\varepsilon \longrightarrow 0+$ with μ_{kl} fixed. By letting $\varepsilon \longrightarrow 0$ we obtain the pure-selection mapping (3.8). Due to (2.13), the same applies to the forward migration matrix $\tilde{M}$.

We consider a compact, convex domain $\Omega \subseteq \mathbb{R}^n$ and two continous mappings

$$x^{'} = f(x) \tag{3.10}$$

and

$$x^{'} = g(x) = f(x) + r(x) \tag{3.11}$$

with $f, g : \Omega \longrightarrow \Omega$. The first equation refers to the original and the second one to the perturbated system, where $r(x) = g(x) - f(x)$ denotes the perturbation or coupling term which is small in a sense to be specified.

We say that a fixed point y of f is locally stable if for every neighborhood U of y there is a neighborhood $V \subseteq U$ of y, such that $f(\bar{V}) \subseteq V$.

The following Theorem by Karlin and McGregor ([6], p. 227) does not yet say anything about the uniqueness or stability of the fixed point of the purturbated system (3.11), but it gives a sufficient condition under which it exists.

Theorem 3.5. *Assume that f,g and r are as defined in (3.10) and (3.11). Further, let y be a fixed point of (3.10). Suppose that for some norm and some $\delta > 0$ the set*

$$V(\delta) = \{x \in \mathbb{R}^n : ||x - y|| \leq \delta\} \cap \Omega \tag{3.12}$$

satisfies the condition

$$x \in V(\delta) \Rightarrow ||f(x) - y|| \leq c||x - y||, \tag{3.13}$$

where $0 \leq c < 1$. Then the perturbated system (3.11) maps $V(\delta)$ into itself and has a fixed point in $V(\delta)$ provided

$$\max_{x \in V(\delta)} ||r(x)|| < (1 - c)\delta. \tag{3.14}$$

The condition (3.13) describes local stability in a more general form. The small neighborhood $V(\delta)$ is a region of stability or in other words, a region of no escape for the slightly purturbated system (3.11) and Theorem 3.5 asserts the existence of at least one fixed point of (3.11) in $V(\delta)$. We now present a criteria ([6], p. 229) under which there will exist a norm satisfying the condition of (3.13).

Lemma 3.6. *Assume that f is as defined in (3.10) and has a fixed point y. Further, suppose that in a neighborhood U of y, continuous first-order partial derivatives exist, and the eigenvalues λ of the matrix*

$$f^{'}(x) = \left(\frac{\partial f_i(x)}{\partial x_j}\right)_{x \in U} \tag{3.15}$$

satisfy $|\lambda| < 1$, which implies that y is locally asymptotically stable. Then there exist $\delta > 0$, $0 \leq c < 1$ and a norm, such that condition (3.13) holds.

In order to show that the fixed point in $V(\delta)$ is unique, we consider a family of continuous mappings

$$x^{'} = f(x, \theta). \tag{3.16}$$

Depending on a parameter θ, with $\theta \in H \subseteq \mathbb{R}^K$ and $\theta_0 \subseteq H$ being the limiting point such that

$$f(x, \theta_0) = f(x). \tag{3.17}$$

Further, we assume that (3.16) is defined on an open neighborhood V of Ω and the partial first-order derivatives exist on V for every $\Omega \subseteq H$. Thus, the matrix

$$f^{'}(x, \theta) = \left(\frac{\partial f^{(i)}(x, \theta)}{\partial x_i} \right) \tag{3.18}$$

exists and is continuous in (x, θ). We set the perturbation term

$$r(x) = f(x, \theta) - f(x, \theta_0) \tag{3.19}$$

for θ sufficiently close to θ_0, such that

$$g(x) = f(x, \theta_0) + r(x) = f(x, \theta). \tag{3.20}$$

Additionally, we suppose that

$$\max_{x \in \Omega}(||r(x)|| + ||r^{'}(x)||) < \varepsilon \tag{3.21}$$

for sufficiently small ε.

By using the implicit function theroem of advanced calculus, it can now be shown that there exists exactly one fixed point with weak migration in the neighborhood of each fixed point without migration and that there are no other stable equilibria. In this context θ corresponds to the backward migration matrix M, and θ_0 to the identity matrix. From Karlin and McGregor ([6], p. 231) and from Bürgers lecture notes [3] we obtain the following Theorem.

Theorem 3.7. *Suppose that f, g and r are as defined in (3.17), (3.20) and (3.19). We further assume that (3.17) has exactly the fixed points $y_1, \dots, y_K$ in Ω and each of them is hyperbolic, thus, the eigenvalue of $f^{'}(y_k, \theta_0)$ is $\neq 1$ for every y_k. Then $g(x)$ admits at most K fixed points $z_1, \dots, z_K$ in Ω, with each z_i in a neighborhood of y_i.*

Moreover, if y_i is locally stable for the original system (3.17), then z_i in Ω certainly exists in a neighborhood of y_i, and is locally stable for the perturbated system (3.20).

If y_i is locally unstable, then if z_i exists in Ω, it is also locally unstable.

Thus, the existence of a locally stable equilibrium point is a qualitative feature preserved under small perturbations. Further, we also have global convergence, hence the solution of (2.9) with weak migration converges to one of the equilibrium points $z_1, \dots, z_K$.

The mean fitness $\bar{w}$ is one of the most important quantities in population genetics, since it measures the capacity of a population to survive and reproduce. To investigate its behavior for (2.9) we define it as

$$\bar{w}(p) = \chi(\bar{w}_1(p^{(1)}, \dots, \bar{w}_k(p^{(k)}), \tag{3.22}$$

where χ is a strictly increasing function of $\bar{w}_k$ for every $k \in \mathcal{K}$. For the pure-selection mapping (3.8) Fisher's Fundamental Theorem of Natural Selection states among other things that the mean fitness $\bar{w}_k(p^{(k)})$ in each deme is monotone nondecreasing and the single-generation change $\Delta\bar{w}_k = 0$ only at equilibrium. If p is bounded away from the equilibria of (3.8) then $\Delta\bar{w}(p) > 0$ for sufficiently small $\varepsilon > 0$. If p is close to an equilibrium, however, the mean fitness may decrease ([13], p.28-29).

3.5 Strong Migration

In this section we assume that migration is strong and dominates selection. Therefore, we can presume that selection is weak and that the fitness values can be calculated as

$$w_{ij,k} = 1 + \varepsilon r_{ij,k}, \tag{3.23}$$

with $r_{ij,k}$ fixed for every $i, j \in \mathcal{J}$ and every $k \in \mathcal{K}$, where s denotes the selection intensity. Thus, for the weak selection or strong migration limit $\varepsilon \longrightarrow 0+$. Nagylaki and Lou showed ([13], p. 29-31) that in this case, the allelic frequencies can converge to an internal, globally stable equilibrium. Before we present this statement in Theorem 3.8, we summarize some necessary assumptions.

We fix the backward migration matrix M and suppose that it is ergodic, thus, irreducible and aperiodic. The irreducibility of M signifies that $m_{kk} > 0$ for at least one $k \in \mathcal{K}$. Irreducibility suffices for aperiocity of M and therefore pathological cyclic behavior cannot occur. It follows that the maximal eigenvalue 1 of M is simple and exceeds every other eigenvalue in modulus. It is obvious that the maximal left eigenvector to the eigenvalue 1, $\alpha \in \mathrm{int}\Delta_k$, satisfies $\alpha^T M = \alpha^T$. Speaking in terms of a Markov chain, α is the unique stationary distribution, where M denotes the transition matrix. One can show that α is only dependent on the relative migration rates. In the case of conservative migration we have $\alpha = c$.

We average the gene frequencies $p_{i,k}$ over deme K with respect to α:

$$P_i = \alpha^T p_i, \qquad P = (P_1, \dots, P_J)^T \in \Delta_J. \tag{3.24}$$

We now denote the deviation of the frequency of allele A_i in niche k, $p_{i,k}$, from the averaged gene frequency, P_i by

$$q_{i,k} = p_{i,k} - P_i. \tag{3.25}$$

Recalling that $u = (1, \dots, 1)^T \in \mathbb{R}^K$ and according to our proceedings in (2.5) we define

$$\begin{aligned} q_i &= p_i - P_i u \in \mathbb{R}^K, \\ q^{(k)} &= p^{(k)} - P \in \mathbb{R}^J, \\ q &= (q^{(1)}; \dots q^{(K)})^T \in \mathbb{R}^{JK}, \end{aligned} \tag{3.26}$$

which refer to the differences of the frequency of A_i in each deme, the gene frequency in deme k and all gene frequencies, with the averaged gene frequencies.

Further, we introduce the average selection coefficients of $A_i A_j$, A_i and the entire population:

$$\begin{aligned} \rho_{ij} &= \sum_k v_k r_{ij,k}, \\ \rho_i(P) &= \sum_j \rho_{ij} P_j, \\ \bar{\rho}(P) &= \sum_{ij} \rho_{ij} P_i P_j. \end{aligned} \tag{3.27}$$

By rescaling time according to $\tau = st$, Nagylaki and Lou ([13], p. 29) derived the strong migration or weak selection limit of (2.9) which is given by the following differential equation

$$\begin{aligned} \frac{dP_i}{d\tau} &= P_i[\rho_i(P) - \bar{\rho}(P)], \\ q &= 0. \end{aligned} \tag{3.28}$$

Due to the suitibly averaged gene frequencies and fitnesses, a simple panmictic system is approximated if there is strong migration. Since $q = 0$, we see that the quantities of the gene frequency deviations among demes tend to become smaller as migration gets stronger.

By using the assumptions above, Nagylaki and Lou formulated and proved the corresponding results as they are stated for weak migration in Theorem 3.7, for strong migration ([13], p. 30-31). The original system is given by (3.28) whereas the perturbated system is (2.9) with strong migration and fitness values as defined in (3.23).

Theorem 3.8. *Suppose that (2.9) holds, the backward migration matrix M is fixed and $s > 0$ is sufficiently small. Moreover, we assume that every equilibrium of (3.28) is hyperbolic. Then*

(i) the set of equilibria $\Sigma_0 \subset \Delta_J^K$ of (3.28) contains only isolated points, as does the set of equilibria $\Sigma_s \subset \Delta_J^K$ of (2.9). As $s \longrightarrow 0$, each equilibrium in Σ_s converges to the corresponding equilibrium in Σ_0.

(ii) in the neighborhood of each equilibrium point in Σ_0, there exists exactly one equilibrium point in Σ_s. The stability of each equilibrium in Σ_s is the same as that of the corresponding equilibrium in Σ_0; i.e, each pair is either asymptotically stable or unstable.

(iii) the solution $p(t)$ of (2.9) converges to one of the equilibrium points in Σ_s.

It can further be seen that all the strong migration results depend on M only through averages, in which deme k has weight α_k. So in the case of conservative migration, the weighting is by c_k and, therefore, under conservative migration all trace of population subdivision disappears.

3.6 Uniform Selection

We investigate the selection-migration model under uniform selection, which means that the fitnesses of an specific allele are the same in every niche, and, therefore, no genetic indication of a population structure can be found. So we assume that the fitnesses are deme independent and posit for this section that $w_{ij,k} = w_{ij}$ for every $i, j \in \mathcal{J}$ and for every $k \in \mathcal{K}$. Further, an equilibrium $\hat{p} \in \Delta_J^K$ is called uniform if $\hat{p}^{(k)} \in \Delta_J$ is independent of k. So obviously, also in the presence of an uniform equilibrium, there is no trace of population structure.

In ([13], p. 33) Nagylaki and Lou formulate and prove a sufficient condition under which there exists a uniform equilibrium in the selection-migration model (2.9):

Theorem 3.9. *Suppose that (2.9) holds and every equilibrium of (3.8) is hyperbolic. If* $\hat{p} \in \Delta_J^K$ *is an uniform equilibrium of (3.8), then* $\hat{p}$ *is an equilibrium of (2.9), and it is either asymptotically stable for both (3.8) and (2.9), or unstable for both systems.*

We see that generically, migration does not change the local stability of uniform equilibria. The ultimate rate of convergence to $\hat{p}$ is determinded entirely by selection and is independent of migration.

For uniform selection the Levene model simplifies to pure selection.

CHAPTER 4

SPECIAL CASES WITH EXAMPLES

In this chapter we study some examples illustrating the general results we established in Chapter 3. The sources, from which the examples are taken, are enclosed at the end of each example. We implemented some of them in Octave, to derive a better insight into their assertions. The examples are categorized according to the number of alleles and demes, respectively.

4.1 Two Alleles and Two Demes

The two examples discussed in this section concern weak migration and uniform selection, respectively. We consider two diallelic demes, with the two alleles A and a.

Example 4.1. According to Theorem 3.7, an unstable boundary equilibrium under the pure-selection mapping (3.8) can disappear if we introduce weak migration. Let us therefore consider overdominance in both demes. The unstable boundary equilibria $\hat{p} = (\hat{p}^{(1)}, \hat{p}^{(2)}) = (1,0;0,1)^T$ and $(0,1;1,0)^T$ of the pure-selection mapping do not survive purturbations, since if we introduce a weak migration flow, these equilibria move outside of the simplex Δ_J^K ([13], p. 28).

Example 4.2. We suppose uniform selection, thus, the fitnesses of allele A are identical in the two niches, the same applies to allele a. Further we assume an underdominant selection pattern. Then the pure-selection mapping in a subdivided population (3.8), obviously, reduces to the pure selection equation independent of k which has a unique unstable internal equilibrium with the equilibrium frequency $p = p_k = p_{1,k}$ of allele A in $(0,1)$. The two fixation states $p = 0$ and $p = 1$ are asymptotically stable. Theorem 3.9 tells us that $\hat{p} = (p, 1-p; p, 1-p)$ is an unstable internal equilibrium of the general selection migration model (2.9), and that the boundary equilibria $(1,0;1,0)^T$ and $(0,1;0,1)^T$ are asymptotically stable fixation equilibria ([13], p. 34).

4.2 Two Alleles and Multiple Demes

We present an expample concerning once again Theorem 3.7 about weak migration. Once more, we consider two alleles A and a. The number of niches shall be K.

Example 4.3. We assume that there is underdominance in every niche and investigate the allelic frequency of allele A in niche k which is $p_k = p_{1,k}$. Without migration, there exist three equilibria in every niche. The two vertices $\hat{p}_k = 0$ and $\hat{p}_k = 1$ are locally asymptotically stable in every niche, and the internal equilibrium $\hat{p}_k = q_k$ is unstable in every deme. Thus, we have 3^k equilibria of which 2^k, with $p_k \in \{0, 1\}$, are locally asymptotically stable. Obviously, every equilibrium is hyperbolic and therefore, Theorem 3.7 can be applied. Thus, if we introduce a weak migration flow the equilibria are preserved and the stable ones move inside, except the two global fixation states $\hat{p} = (0, \dots, 0)$ and $\hat{p} = (1, \dots, 1)$. Consequently, for weak migration there exist 2^k local asymptotically stable equilibria of which $2^k - 2$ are located in the internal of the simplex (cf. [3]).

4.3 Multiple Alleles and Multiple Demes

For the case of multiple alleles and multiple demes, we present an example that leads to the atypical case of single-generation convergence. Subsequently, we give two examples of fully protected polymorphisms by applying Theorem 3.7.

Example 4.4. We suppose that the number of alleles equals the number of niches, thus $J = K$. Further we assume that every heterozygote is lethal, which means $w_{ij,k} = 0$ for every $i \neq j$ and that the homozygotes A_iA_i can survive only in deme i for every $i \in \mathcal{J}$. Therefore, the fitness values can be written as

$$w_{ij,k} = \alpha_i \delta_{ij} \delta_{ik} \tag{4.1}$$

for some $\alpha_i > 0$. The mean fitness of allele A_i in niche k (2.6) and the mean fitness of all individuals in k (2.7) becomes

$$w_{i,k} = \sum_j \alpha_i \delta_{ij} \delta_{ik} p_{j,k} = \alpha_i \delta_{ik} p_{i,k} \tag{4.2}$$

and

$$\bar{w}_k = \sum_{i,j} \alpha_i \delta_{ij} \delta_{ik} p_{i,k} p_{j,k} = \alpha_k p_{k,k}^2, \tag{4.3}$$

respectively. Substituting (4.2) and (4.3) into (2.9) yields

$$p_{i,k}^{'} = \sum_l m_{kl} p_{i,l} \frac{\alpha_i \alpha_{il} p_{i,l}}{\alpha_l p_{l,l}^2} = m_{ki} \tag{4.4}$$

and consequently, $p_{i,k}(t) = m_{ki}$ for $t \geq 1$. Thus, the allelic frequency of A_i in deme k equals the probability of being in k and coming from niche i. Due to the heterozygote's lethality, this probability stays the same after one generation and we have an atypical, single-generation convergence ([14], p. 132-133).

Example 4.5. We suppose that the number of demes equals or exceeds the number of alleles, thus $J \geq K$. Further, we choose a selection scheme such that, without migration, every equilibrium is hyperbolic and that there exists a globally asymptotically stable equilibrium $\hat{p}$ with

$$\hat{p} = \begin{cases} \hat{p}_{i,k} > 0, & \text{if } i \in \mathcal{J}^{(k)} \\ \hat{p}_{i,k} = 0, & \text{otherwise} \end{cases} \tag{4.5}$$

for every $k \in \mathcal{K}$ and where the $J^{(k)}$ are a decomposition of J, i.e.,

$$\mathcal{J} = \bigcup_{k=1}^{K} \mathcal{J}^{(k)}, \qquad \mathcal{J}^{(k)} \neq 0, \qquad \mathcal{J}^{(k)} \cap \mathcal{J}^{(l)} = \varnothing \tag{4.6}$$

for every $k, l \in \mathcal{K}$ such that $k \neq l$. Thus, alleles from $\mathcal{J}^{(k)}$ can be found in niche k if and only if $p = \hat{p}$ and each allele is present in exactly one deme. Theorem 3.7 states that for weak migration there exists exactly one equilibrium $\tilde{p}$ close to $\hat{p}$ and $p(t) \longrightarrow \tilde{p}$ as $t \longrightarrow \infty$. If M is irreducible, we obtain that $\tilde{p}_{i,k} > 0$ for every $i \in \mathcal{J}$ and every $k \in \mathcal{K}$. Therefore, every allele is present in each deme and a globally asymptotically stable internal equilibrium exists. ([14], p. 133).

Example 4.6. We assume no dominance (2.18) and $J \geq K$. Every allele shall be the fittest in at least one deme, thus

$$\mathcal{K}^{(i)} = \{k \in \mathcal{K} : v_{i,k} > \max_{j : j \neq i} v_{j,k}\}, \tag{4.7}$$

and

$$\mathcal{K} = \bigcup_{i=1}^{J} \mathcal{K}^{(i)}, \qquad \mathcal{K}^{(i)} \neq 0, \qquad \mathcal{K}^{(i)} \cap \mathcal{K}^{(j)} = \varnothing \tag{4.8}$$

for every $i, j \in \mathcal{J}$, such that $i \neq j$. Without migration it follows from (2.8) and (2.19) that

$$p'_{i,k} = p_{j,k} \frac{v_{j,k} + \bar{v}_k}{\bar{v}_k}. \tag{4.9}$$

If $k \in \mathcal{K}^{(i)}$, then $v_{i,k} > v_{j,k}$ for every $j \in \mathcal{J}$ and consequently $v_{i,k} > \bar{v}_k$, since allele i is the fittest allele in $\mathcal{K}^{(i)}$. We see that

$$p'_{i,k} = p_{i,k} \frac{v_{i,k} + \bar{v}_k}{2\bar{v}_k} > p_{i,k} \tag{4.10}$$

for $p_{j,k} \neq 0, 1$. As $p_{i,k} \longrightarrow 1$

$$p'_{j,k} \sim p_{j,k} \frac{v_{j,k} + v_{i,k}}{2v_{i,k}} < p_{j.k} \tag{4.11}$$

for every $j \neq i \in \mathcal{J}$. Thus, the equilibrium $\hat{p}$ with $\hat{p}_{i,k} = 1$ if $k \in \mathcal{K}^{(i)}$ and $\hat{p}_{i,k} = 0$ if $k \notin \mathcal{K}^{(i)}$ for every $i \in \mathcal{J}$ is hyperbolic and, with respect to the internal of the simplex, it is globally asymptotically stable. For every $i \in \mathcal{J}$, A_i is eventually fixed in $\mathcal{K}^{(i)}$ and eliminated in all the other niches $\mathcal{K} - \mathcal{K}^{(i)}$. With weak migration, Theorem 3.7 tells us that there exists a globally asymptotically stable equilibrium $\tilde{p}$ close to $\hat{p}$ with $p(t) \longrightarrow \tilde{p}$ as $t \longrightarrow \infty$ and $0 < \tilde{p}_{i,k} < 1$ for every $i \in \mathcal{J}$ and every $k \in \mathcal{K}$. Thus, every allele is present in each deme ([14], p. 133).

CHAPTER 5

THE LEVENE MODEL

In this chapter we study a special case of a selection-migration model, the Levene model, which was first stated 1953 by H. Levene [9]. The main assumption is that migration takes place independently of the deme of origin. Further, mating occurs at random across the local habitat structure and, after reproduction, the population distributes again to K habitats. This kind of migration structure can be approximately found in polychaetes (marine worms) which engage in swarming maneuvers only for mating and then settle back again to available habitats. It might also apply to seabird populations that nest in large rookeries. Further, a number of fish populations (e.g., the American eel and herring) breed together in spawning areas and afterwards, remembering the foregoing population structure, return back to habitats located up various streams ([7], p. 362).

We will see immediately that in the Levene population subdivision model after one generation of migration the allele frequencies in every niche are the same. Consequently, the dynamics become simpler and a more detailed analysis can be provided. Many interesting results and special cases are obtained which can not be established for the general selection-migration pattern.

5.1 Formulation

The general assumptions on the population are as stated in Chapter 1. We just assume that migration is random and individuals disperse independently of their deme of origin, so there exist μ_l such that

$$\tilde{m}_{kl} = \mu_l \tag{5.1}$$

for every $k, l \in \mathcal{K}$, and

$$\sum_l \mu_l = 1. \tag{5.2}$$

For the backward migration rates we get from (2.14) that

$$m_{kl} = \frac{c_l^* \mu_k}{\sum_n c_n^* \mu_k} = c_l^*. \tag{5.3}$$

This relation indicates that, although we have population subdivision in the Levene model, there is no geographical structure, since distance between the niches plays no role in the migrating process. For the niche proportions, we obtain from (2.11)

$$c_k^{**} = \sum_l c_l^* \mu_k = \mu_k. \tag{5.4}$$

So the relative deme sizes after migration are the same in every generation and equal μ_k. Therefore, it is common to assume that the deme proportions remain constant after each generation and, thus, we interpret $c_k = \mu_k$ for every $k \in \mathcal{K}$. For the forward migration rates this assumption leads instantly to

$$\tilde{m}_{kl} = c_l \tag{5.5}$$

for every $l, k \in \mathcal{K}$. It follows from (2.9) and (5.3) that the dynamics of the Levene model,

$$p_{i,k}^{'} = \sum_l c_l^* p_{i,l}^*, \tag{5.6}$$

are independent of k and due to (2.8) it can be written as

$$p_i^{'} = p_i \sum_l c_l^* \frac{w_{i,l}}{\bar{w}_l}. \tag{5.7}$$

Thus, after one generation of migration the zygote gene frequencies are the same in every deme and it suffices to study the allele frequencies $p = (p_1, \ldots, p_J) \in \Delta_J$ ([10], p. 144).

The property for general selection-migration models of not being a Levene model is generic. Thus, the Levene model is a nongeneric case of a selection-migration model. To illustrate this circumstance, we assume the case of two alleles and two niches. In the general selection-migration model, the backward migration matrix is given by

$$M = \begin{pmatrix} 1-m_1 & m_1 \\ m_2 & 1-m_2 \end{pmatrix}. \tag{5.8}$$

Thus, if we fix selection, we can interpret the set of all selection-migration models as points in the $m_1 m_2$ plane, with $0 \leq m_1, m_2 \leq 1$. For every m_1 and m_2 we obtain the corresponding selection-migration model. For the Levene model the backward migration matrix becomes

$$M = \begin{pmatrix} c_1 & c_2 \\ c_1 & c_2 \end{pmatrix}, \tag{5.9}$$

thus $m_1 = c_2$ and $m_2 = c_1$. We can interpret the set of all Levene models as points on the line $c_1 = 1 - c_2$ in the $m_1 m_2$ plane, since $c_1 + c_2 = 1$. For fixed selection, we have generically that $m_1 + m_2 \neq 1$, thus, the set of all Levene models is contained in a set of measure zero. By showing our delineations in Figure 5.1 we want to point out, how specific the special case of the Levene model is, and that the results and examples shown in this chapter concern only a small part of the set of all selection-migration models.

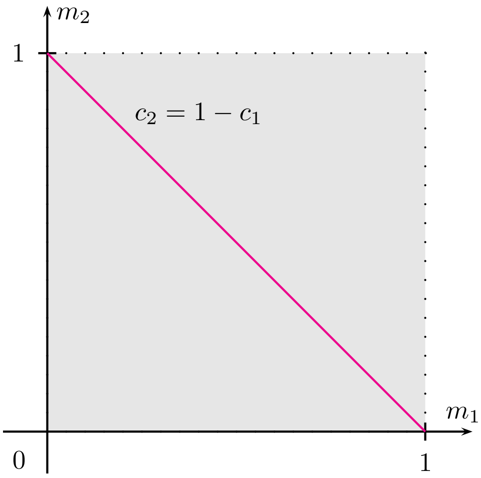

Fig. 5.1: The set of all Levene models in the $m_1 m_2$ plane

Similarly, as we proceeded in Chapter 2 for the general selection-migration model, in the following two subsections, we will study the Levene model under soft and hard selection.

5.1.1 Soft Selection

We recall property (2.15) for soft selection and obviously get from (5.3)

$$m_{kl} = c_l. \tag{5.10}$$

Consequently, from (5.5) we see that

$$m_{kl} = \tilde{m}_{kl} = c_l \tag{5.11}$$

for every $k, l \in \mathcal{K}$. By inserting (5.5) in (5.7) we obtain the Levene dynamics for soft selection

$$p_i^{'} = p_i \sum_l c_l \frac{w_{i,l}}{\bar{w}_l} \tag{5.12}$$

for every $i \in \mathcal{J}$. Again we want to point out that after one generation of migration, each subpopulation involves the same allelic mixture as the whole population. Since we have the same allele proportions in every niche and these do not change during reproduction due to Hardy-Weinberg, we can assume that breeding occurs in a common place and afterwards the population distributes again to K habitats. We always suppose that $c_k > 0$ for every $k \in \mathcal{K}$. In order to write (5.12) in a different way and to show that the population will evolve steadily to an equilibrium, we compute, as done in [3],

$$\begin{aligned} \frac{\partial \bar{w}_l}{\partial p_i} &= \frac{\partial}{\partial p_i} \sum_{j,h} p_j p_h w_{ij,l} \\ &= 2 \sum_j p_j w_{ij,l} \\ &= 2 w_{i,l}. \end{aligned} \tag{5.13}$$

Inserting this relation into the Levene dynamics (5.12) gives

$$\begin{aligned} p_i^{'} &= p_i \sum_k c_k \frac{w_{i,k}}{\bar{w}_k} \\ &= \frac{1}{2} p_i \sum_k \frac{c_k}{\bar{w}_k} \frac{\partial \bar{w}_k}{\partial p_i} \\ &= \frac{1}{2} p_i \sum_k c_k \frac{\partial}{\partial p_i} \ln \bar{w}_k \\ &= \frac{1}{2} p_i \frac{\partial}{\partial p_i} \ln \prod_k \bar{w}_k^{c_k}. \end{aligned} \tag{5.14}$$

We set

$$w^* = \prod_k \bar{w}_k^{c_k} \tag{5.15}$$

which can be interpreted as the geometric mean of the average fitnesses in the various niches. Thus, the Levene dynamics for soft selection (5.12) can be equivalently written as

$$p_i^{'} = \frac{1}{2} p_i \frac{\partial}{\partial p_i} \ln w^* \tag{5.16}$$

which has the form of multiallelic selection in a single, panmictic population ([10], p. 145). Since $\sum_i p_i^{'}$ must still equal 1, we have

$$\sum_i p_i \frac{\partial w^*}{\partial p_i} = 2w^* \tag{5.17}$$

and can rewrite (5.16) as

$$p_i^{'} = \frac{p_i \frac{\partial w^*}{\partial p_i}}{\sum_j p_j \frac{\partial w^*}{\partial p_j}}. \tag{5.18}$$

We now present the inequality of Baum and Eagon [1] which will be used in the subsequent proof that w^* is a Lyapunov function for the Levene model with soft selection ([10], p. 145).

Theorem 5.1. *Let $P(x), x = (x_1, \ldots, x_n) \in \mathbb{R}$ be a homogenous polynomial in x of degree d, with nonnegative coefficients. Let $x \in \Delta_K$ be arbitrary and $y(x) = (y_1(x), \ldots, y_K(x))$ given by*

$$y_k(x) = \frac{x_k \frac{\partial P(x)}{\partial x_k}}{\sum_{n=1}^K x_n \frac{\partial p(x)}{\partial x_n}}. \tag{5.19}$$

Then $P(y(x)) > P(x)$ unless $y(x) = x$.

Theorem 5.2. *The geometric mean fitness w^* is a Lyapunov function for (5.12) which is equivalent to (5.18). Thus, $\Delta w^*(p) = w^*(p^{'}) - w^*(p) \geq 0$ for every $p \in \Delta_J$ and $\Delta w^*(p) = 0$ if and only if p is an equilibrium.*

Proof. Let $\varepsilon > 0$, choose $\delta > 0$ sufficiently small, as it will be specified later, and $\gamma_1, \ldots, \gamma_k \in \mathbb{Q}$ sufficiently close to $c_1, \ldots, c_k$ such that

$$|w(p) - w^*(p)| < \delta \tag{5.20}$$

for every $p \in \Delta_J$, where

$$w(p) = \prod_{k=1}^{K} \bar{w}_k^{\gamma_k} \tag{5.21}$$

and Δ_J is compact. Then there exists a positive integer $l \in \mathbb{N}$, such that $F_\varepsilon(p) := w(p)^l$ is a homogenous polynomial in p with coefficients ≥ 0. Additionally, we choose $\delta > 0$ sufficiently small, such that

$$\left| \frac{\frac{\partial w^*}{\partial p}}{\sum_n p_n \frac{\partial w^*}{\partial p_n}} - \frac{\frac{\partial w(p)}{\partial p}}{\sum_n p_n \frac{\partial w(p)}{\partial p_n}} \right| < \varepsilon. \tag{5.22}$$

This is equivalent to

$$\left| \frac{\frac{\partial w^*}{\partial p}}{\sum_n p_n \frac{\partial w^*}{\partial p_n}} - \frac{\frac{\partial F_\varepsilon}{\partial p}}{\sum_n p_n \frac{\partial F_\varepsilon}{\partial p_n}} \right| < \varepsilon, \tag{5.23}$$

on Δ_J, since

$$\frac{\partial F_\varepsilon}{\partial p} = l w(p)^{l-1} \frac{\partial w(p)}{\partial p} \tag{5.24}$$

and therefore

$$\frac{\frac{\partial F_\varepsilon}{\partial p}}{\sum_n p_n \frac{\partial F_\varepsilon}{\partial p_n}} = \frac{\frac{\partial w(p)}{\partial p}}{\sum_n p_n \frac{\partial w(p)}{\partial p_n}}. \tag{5.25}$$

The inequality of Baum and Eagon now tells us that every F_ε is a Lyapunov function for the dynamics

$$p'_{(\varepsilon),i} = \frac{p_i \frac{\partial F_\varepsilon}{\partial p_i}}{\sum_n p_n \frac{\partial F_\varepsilon}{\partial p_n}}. \tag{5.26}$$

Therefore, also w is a Lyapunov function for (5.26), thus, $w(p'_{(\varepsilon)}) > w(p)$ as long as $p'_{(\varepsilon)} \neq p$.

So we have that $\Delta w(p) \geq 0$ in Δ_J and consequently, $\Delta w^* \geq 0$ in Δ_J. We get $\Delta w^* = 0$ if and only if $p' = p$ (cf. [3]). ☐

So we see that w^* is nondecreasing from generation to generation and remains unchanged only at equilibrium states, as does the mean fitness $\bar{w}$ in a single panmictic population with multiallelic selection.

In this work we focus on soft selection, because as we will see in the following subsection about hard selection, in the Levene model (5.7) reduces to panmixia.

5.1.2 Hard Selection

Using the same argumentation as in Subsection 5.1.1, we suppose that the zygotic distribution c is regulated to constancy, thus $c^{'} = c$. It follows from (2.14) and (5.1) that

$$m_{kl} = c_l^* = c_l \frac{\bar{w}_l}{\bar{w}}. \tag{5.27}$$

Inserting (5.27) in (2.9) gives

$$\begin{aligned} p_{i,k}^{'} &= \sum_l m_{kl} p_{i,l}^* \\ &= \sum_l c_l \frac{\bar{w}_l}{\bar{w}} p_{i,l} \frac{w_{i,l}}{\bar{w}_l} \\ &= \frac{1}{\bar{w}} \sum_l c_l p_{i,l} w_{i,l} \end{aligned} \tag{5.28}$$

which is, as in the case of soft selection, independent of k. So we can write the dynamics for hard selection ([10], p. 146) as

$$p_i^{'} = p_i \frac{\sum_l c_l w_{i,l}}{\bar{w}}. \tag{5.29}$$

If we consider instead of $w_{ij,k}$ the arithmetic mean fitness of A_iA_j, A_i, and the entire population over the niches we get

$$\begin{aligned} z_{ij} &= \sum_k c_k w_{ij,k}, \\ z_i &= \sum_j z_{ij} p_j = \sum_k c_k w_{i,k}, \\ \bar{z} &= \sum_{i,j} z_{ij} p_i p_j = \sum_{ij,k} w_{ij,k} p_i p_j = \bar{w}, \end{aligned} \tag{5.30}$$

such that the dynamics of hard selection (5.29) simplify to

$$p_i^{'} = p_i \frac{z_i}{\bar{z}}. \tag{5.31}$$

This is the classical selction equation for a single random mating population with fitnesses z_{ij}. Thus, the Levene model with hard selection is a special case of the one locus selection model ([10], p. 147). Therefore, $\Delta\bar{w} \geq 0$ and $\Delta\bar{w} = 0$ only at equilibrium. So the mean fitness is nondecreasing and the population converges to some equilibrium point or surface.

5.1.3 No Dominance

If there is soft selection and no dominance, we obtain from (2.18) and (5.12)

$$p_i^{'} = \frac{1}{2} p_i \left(\sum_k c_k \frac{v_{i,k}}{\bar{v}_k} + 1 \right) \tag{5.32}$$

with

$$\bar{v}_k(p) = \sum_i v_{i,k} p_i. \tag{5.33}$$

Furthermore, the change in the allele frequency is given by

$$\Delta p_i = p_i^{'} - p_i = p_i \sum_k c_k \frac{v_{i,k} - \bar{v}_k}{2\bar{v}_k} = \frac{1}{2} p_i \sum_k c_k (\frac{v_{i,k}}{\bar{v}_k} - 1). \tag{5.34}$$

If there is no dominance and hard selection, the fittest allele will be ultimately fixed. Since we obtained from the previous subsection that under hard selection the Levene model reduces to the one locus selection model, we get from $\Delta \bar{w} \geq 0$ and $\bar{w} = 0$ only at equilibrium, and no dominance, that $\bar{w}$ is an increasing function of p on the simplex. Therefore, the favoured allele eventually goes to fixation and selection removes all genetic viability ([2], p. 14).

5.2 General Results

Similar to our approach in Chapter 3 for the general selection-migration model, we now give an overview of the general results in the Levene model. We start by showing an interesting result about the weak selection limit ([11], p. 302).

Proposition 5.3. *In the weak selection limit, soft and hard selection, and therefore also panmixia, are equivalent.*

Proof. We set $w_{ij,k} = 1 + s r_{ij,k}$ with $s > 0$ which denotes the selection intensity. We rescale time according to $\tau = st$ and set $\Pi_i(\tau) = p_i(t)$. Further, we suppose that

$$r_{i,k} = \sum_j r_{ij,k} \Pi_j \tag{5.35}$$

and

$$\bar{r}_k = \sum_i r_{i,k} \Pi_i = \sum_{i,j} r_{ij,k} \Pi_i \Pi_j. \tag{5.36}$$

Obviously, the average mean fitness of an allele in niche k is

$$w_{i,k} = 1 + s r_{i,k} \tag{5.37}$$

and the average mean fitness of the population in niche k is

$$\bar{w}_k = 1 + s \bar{r}_k. \tag{5.38}$$

By inserting the assumptions above in the Levene model with soft selection (5.12) we see that the change in the allelic frequency is

$$\Delta p_i = s p_i \sum_k c_k \frac{r_{i,k - \bar{r}_k}}{1 + s \bar{r}_k}. \tag{5.39}$$

By letting $s \longrightarrow 0$, we can now calculate

$$\begin{aligned}
\frac{\partial \Pi_i}{\partial \tau} &= \lim_{s \to 0} \frac{\Pi_i(\tau + s) - \Pi_i(\tau)}{s} \\
&= \lim_{s \to 0} \frac{1}{s} \Delta p_i(t) \\
&= \lim_{s \to 0} p_i \sum_k c_k \frac{r_{i,k} - \bar{r}_k}{1 + s\bar{r}_k} \\
&= \Pi_i \sum_k c_k (r_{i,k} - \bar{r}_k) \\
&= \Pi_i (\sum_k c_k r_{i,k} - \sum_k c_k \bar{r}_k) \\
&= \Pi_i (z_i - \bar{z}) \qquad (5.40)
\end{aligned}$$

which is precisely the result for hard selection and panmixia (cf. [3]). ☐

An important result for the Levene model is the following (cf. [3]):

Corollary 5.4. *In the Levene model (with soft or hard selection) the gene frequencies converge to some equilibrium (point or surface) for all inital conditions.*

Proof. Due to Theorem 5.2, if $\hat{p}$ is an equilibrium, then $w^*(\hat{p}) \geq w^*(p)$ and $w^*(\hat{p}) = w^*(p)$ only at equilibrium. Therefore, every trajectory of (5.7) converges to some equilibrium (point or manifold). ☐

We now know that in the Levene model every trajectory converges to some equilibrium and we are interested under which conditions this equilibrium (point or surface) is unique.

5.2.1 Concavity

We investigate the behavior of

$$F(p) = \ln w^*(p) = \sum_k c_k \ln \bar{w}_k(p) \qquad (5.41)$$

and derive a sufficient condition for the existence of a unique stable equilibrium in the Levene model. We will start with this substantial theorem by Nagylaki and Lou ([11], p. 302) and then delineate under which circumstances its requirements are fulfilled and, consequently, it can be applied.

Theorem 5.5. *If $F(p)$ is concave, then there exists exactly one stable equilibrium (point or manifold) and it is globally attracting. If there exists an internal equilibrium, it is the global attractor.*

Proof. Since F is concave, $\Delta F \geq 0$ and $\Delta F = 0$ only at equilibrium, an internal equilibrium, provided it exists, is a global maximum of F and, therefore, globally attracting.

To show the first statement of the Theorem, we suppose that there exist two stable equilibria on the boundary of the simplex Δ_J. We choose a point from each of them and join them by a line. Since F is concave, it must be constant along this line and therefore, it must be an internal equilibrium. It follows from the first part of the proof that this manifold is unique and globally stable. ☐

Thus, we are now interested in conditions under which $F(p)$ is concave ([11], p. 302).

Corollary 5.6. *If $\bar{w}_k(p)$ is concave for every $k \in \mathcal{K}$, than $F(p)$ is concave.*

Proof. The conjunction of a concave function $f : \mathbb{R}^J \longrightarrow \mathbb{R}$ and a monotone increasing function $g : \mathbb{R} \longrightarrow \mathbb{R}$ is concave, since for every $p, q \in \mathbb{R}^J$ and $\alpha, \beta > 0$ with $\alpha + \beta = 1$ we have

$$f(\alpha p + \beta q) \geq \alpha f(p) + \beta f(q) \tag{5.42}$$

and because g is monotone we obtain

$$\begin{aligned} g(f(\alpha p + \beta q)) &\geq g(\alpha f(p) + \beta f(q)) \\ &\geq \alpha g(f(p)) + \beta g(f(q)), \end{aligned} \tag{5.43}$$

which is the definition for concavity of $g \circ f$. Therefore, also $\ln \bar{w}_k$ is concave and consequently F. ☐

The following Theorem ([11], p. 302) will be applied in some cases later on:

Theorem 5.7. *If in every deme there is no dominance or if we suppose that without migration there is a globally attracting internal equilibrium in every deme, then $F(p)$ is concave.*

Proof. If there is no dominance, then it follows from (2.18) and (5.33) that $\bar{w}_k = 2\bar{v}_k$, where $\bar{v}_k$ is linear in every niche. Therefore, $\ln \bar{w}_k = \ln 2 + \ln \bar{v}_k$ is concave for every $k \in \mathcal{K}$ and due to Corollary 5.6 so is F.

If there is, without migration, a globally attracting internal equilibrium in niche k, then $\bar{w}_k$ has its maximal value there and the $\bar{w}_k$ are concave for every $k \in \mathcal{K}$. Since $\Delta\bar{w}_k \geq 0$ and $\Delta\bar{w}_k = 0$ only at equilibrium, stable equilibria can be found only where $\bar{w}_k$ reaches its maximum value. Again, due to Corollary 5.6 F is concave. ☐

In the special case of two alleles, Bürger (cf. [3]) formulated and proved the following Lemma:

Lemma 5.8. *Suppose there are two alleles, then $\ln \bar{w}_k$, and consequently also $F(p)$, is concave if and only if*

$$u_k v_k \leq 1 + (1 - v_k)^2 \qquad \textit{and} \qquad v_k \leq 1 \tag{5.44}$$

or

$$u_k v_k \leq 1 + (1 - u_k)^2 \qquad \textit{and} \qquad u_k \leq 1. \tag{5.45}$$

We will treat the Levene model with two alleles separately and in greater detail in Section 5.3.

5.2.2 Equilibria If There Is No Dominance

In this subsection we study evolution in the Levene model in the absence of dominance. Nagylaki and Lou proved that Theorem 3.3, which states that without dominance, the number of demes is a generic upper bound on the number of alleles present at equilibrium, is valid also for the Levene model ([11], p. 306). Further we determine explicitly the equilibrium point, which is only possible if $J = K$.

Theorem 5.9. *Theorem 3.3 applies to the Levene model.*

Proof. We assume no dominance and obtain from (5.34) that an internal equilibrium of the Levene dynamics must satisfy

$$\sum_k c_k \frac{v_{i,k}}{\bar{v}_k} = 1 \tag{5.46}$$

for every $i \in \mathcal{J}$, in order to derive $p^{'} = p$. Let us suppose that $\hat{\bar{v}}_k = \bar{v}_k(\hat{p})$ is the value at such an internal equilibrium. We linearize (5.46) by substituting

$$x_k = \frac{c_k}{\hat{\bar{v}}_k}. \tag{5.47}$$

Then we get the system

$$\sum_k v_{i,k} x_k = 1 \tag{5.48}$$

for every $i \in \mathcal{J}$, which consists of J inhomogenous, linear equations for K unknown variables $x = (x_1, \ldots, x_K)$. Furthermore, we see that

$$\bar{v_k}(\hat{p}) = \sum_i v_{i,k} \hat{p}_i = \frac{c_k}{x_k} \tag{5.49}$$

for every $k \in \mathcal{K}$. Since generically the rank of a $n \times m$ matrix equals $\min(n, m)$, a solution of (5.48) exists generically only if $J \leq K$ (cf. [3]). ☐

In general, if $J < K$, it is not posssible to solve (5.46) for an internal equilibrium. We can have a general solution only in the case when the number of alleles equals the number of demes.

So let us suppose this is the case and $J = K$. Let V be a $J \times J$ matrix such that $(V)_{ki} = v_{i,k}$. Thus, row k corresponds to deme k and column i to allele A_i. The adjungate matrix of V is adj$V$ and

$$\mathrm{adj}V = \det(V) \cdot V^{-1} \tag{5.50}$$

provided that det$V \neq 0$, which holds generically. Now the following Theorem by Nagylaki and Lou ([12], p. 407) gives us the general solution for the equilibrium.

Theorem 5.10. *We posit that* $\mathrm{detV} \neq 0$. *An isolated, internal equilibrium point exists if and only if*

$$\hat{p}_i = \sum_k \frac{c_k}{d_k} (\mathrm{adjV})_{\mathrm{ik}} > 0 \tag{5.51}$$

for every $i \in \mathcal{J}$*, with*

$$d_k = \sum_j (\mathrm{adjV})_{\mathrm{jk}}. \tag{5.52}$$

Then $\hat{p} = (\hat{p}_1, \ldots, \hat{p}_J)$ *is an equilibrium and globally asymptotically stable.*

Proof. We rewrite (5.48) and (5.49) in matrix form and get

$$V^T x = u, \qquad V\hat{p} = \hat{\hat{v}} \tag{5.53}$$

with $u = (1, \ldots, 1)^T$. We still use the same substitution (5.47) as in the proof of Theorem 5.9. Let us assume that $\det V \neq 0$. By using (5.53), (5.47), (5.53), (5.50) and (5.52) successively, we obtain as in [3]

$$\begin{aligned} \hat{p}_i &= \sum_k (V^{-1})_{ik} \hat{\hat{v}}_k = \sum_k (V^{-1})_{ik} \frac{c_k}{x_k} = \sum_k (V^{-1})_{ik} \frac{c_k}{[(V^T)^{-1}u]_k} = \\ &= \sum_k c_k \frac{(\mathrm{adj}V)_{ik}/\det V}{[\mathrm{adj}V^T u]_k/\det V} = \sum_k c_k \frac{(\mathrm{adj}V)_{ik}}{\sum_j (\mathrm{adj}V)_{jk}} = \sum_k \frac{c_k}{d_k} (\mathrm{adj}V)_{ik}. \end{aligned} \tag{5.54}$$

From the definition of d_k we see that

$$\sum_i \hat{p}_i = \sum_k \frac{c_k}{d_k} \sum_i (\mathrm{adj}V)_{ik} = \sum_k c_k = 1. \tag{5.55}$$

So an isolated, internal equilibrium $\hat{p}$ exists if and only if (5.51) holds for every $i \in \mathcal{J}$. The global asymptotic stability follows from Theorem 5.5. □

5.2.3 Arbitrarily Many Alleles at Equilibrium

As executed by Nagylaki and Lou, we show that the assumption of genericity in Theorems 3.3 and 5.9 is essential. In the nongeneric case we will see that even without dominance and only two demes arbitrarily many alleles can be maintained in the equilibrium. The proofs presented are essentially due to Nagylaki and Lou ([11], p. 310-312), but worked out in greater detail by consulting Bürgers lecture notes [3].

Let us suppose that the genotype and deme dependence of the selection coefficients are independent, so we can write

$$w_{ij,k} = 1 + g_k r_{ij} \tag{5.56}$$

for some g_k and r_{ij} with $i, j \in \mathcal{J}$ and $k \in \mathcal{K}$. The choice of 1 in (5.56) does not affect the allelic frequencies, since we have $w_{ij,k}/\bar{w}_k$ in (5.12). The variables g_k and r_{ij} denote deme dependence and genotype dependence, respectively. We further assume that the number of alleles J and the number of niches K are arbitrary.

We define

$$r_i = \sum_j r_{ij} p_j, \qquad \bar{r} = \sum_{i,j} r_{ij} p_i p_j \tag{5.57}$$

and the selection coefficients become

$$w_{i,k} = 1 + g_k r_i, \qquad \bar{w}_k = 1 + g_k \bar{r}. \tag{5.58}$$

Further we set

$$r^* = \min_{p\in\Delta_J} \bar{r}(p), \qquad r^{**} = \max_{p\in\Delta_J} \bar{r}(p) \tag{5.59}$$

and

$$H(y) = \sum_k \frac{c_k g_k}{1+g_k y}, \qquad \forall y \in \mathbb{R}. \tag{5.60}$$

Nagylaki and Lou proved that under the assumptions above, an attracting internal manifold of equilibria can exist ([11], p. 311).

Theorem 5.11. *Under the assumption (5.56) and with J and K arbitrary, we have the following equilibria in the Levene model:*

(i) Every equilibrium of a panmictic population with selection coefficients r_{ij} is an equilibrium.

(ii) If $H(r^*) > 0 > H(r^{**})$, then there exists a unique solution of the equation $H(y) = 0$ in (r^*, r^{**}), which we denote by $\hat{y}$, and the conic $\bar{r} = \hat{y}$ is an attracting, internal manifold of equilibria.

Proof. We first prove part (i). From (5.34) we get that

$$\begin{aligned} \Delta p_i &= p_i \sum_k c_k \frac{w_{i,k} - \bar{w}_k}{\bar{w}_k} = P_i \sum_k c_k \frac{g_r(r_i - \bar{r})}{1+g_k\bar{r}} \\ &= p_i(r_i - \bar{r})H(\bar{r}) \end{aligned} \tag{5.61}$$

which immediately shows (i).

Obviously, every nonpanmictic equilibrium must satify $H(\bar{r}) = 0$. From (5.41) and (5.56) we see that we can define

$$\Phi(\bar{r}) = F(p) = \sum_k c_k \ln(1 + g_k\bar{r}). \tag{5.62}$$

Differentiating Φ yields

$$\frac{\partial \Phi(y)}{\partial y} = H(y), \tag{5.63}$$

and therefore, nonpanmictic equilibria can exist only where Φ is constant. By differentiating (5.63) once more, we obtain

$$\frac{\partial^2 \Phi}{\partial y}(y) = \frac{\partial H}{\partial y}(y) = -\sum_k \frac{c_k g_k^2}{(1+g_k y)^2} < 0 \tag{5.64}$$

and can conclude that $\Phi(y)$ is strictly concave and $H(y)$ strictly monotone decreasing. Since we assumed that $H(r^*) > 0 > H(r^{**})$ and H is strictly monotone decreasing, it follows that $\hat{y}$ is uniquely defined in (r^*, r^{**}).

Further, the strict concavity of Φ in (r^*, r^{**}) implies that the equilibria, which are given by $F(p) = \hat{y}$, are attracting (cf. [3]). □

As we have shown in Subsection 5.1.2, the Levene model with hard selection is equivalent to panmixia, and therefore, equilibria of type (ii) do not exist in that case.

We now consider the case of no dominance. Consequently, there exist s_i such that we can write

$$r_{ij} = s_i + s_j \tag{5.65}$$

for every $i, j \in \mathcal{J}$. Furthermore we have

$$r_i = s_i + \bar{s}, \qquad \bar{r} = 2\bar{s} \tag{5.66}$$

with

$$\bar{s} = \sum_i s_i p_i. \tag{5.67}$$

For arbitrary J and K Nagylaki and Lou showed that again in the nongeneric case, there exists an attracting, internal manifold of equilibria without dominance ([11], p. 312).

Theorem 5.12. *Suppose there is no dominance and $H(2s_i) \neq 0$ for every $i \in \mathcal{J}$. Without loss of generality we assume that $s_1 > s_2 > \cdots > s_J$. Then the global attractor in the Levene Model is one of the following:*

(i) $p_1 = 1$ *if* $H(2s_1) > 0$;

(ii) $p_J = 1$ *if* $H(2s_J) < 0$;

(iii) the hyperplane $2\bar{s}(p) = \hat{y}$ *if* $H(2s_J) > 0 > H(2s_1)$, *where* $\hat{y}$ *is the unique solution of the equation* $H(y) = 0$ *in* $(2s_J, 2s_1)$.

Proof. Theorems 5.7 and 5.5 tell us that there always exists a global attractor. Due to the previous Theorem 5.11 and under the assumption that the attractor is internal, it must be given by the conic $F(p) = 2\bar{s}(p) = \hat{y}$. Again Theorem 5.11 tells us that in order for this internal attractor to exist, $H(r^*) > 0 > H(r^{**})$ needs to hold, which is equivalent to $H(2s_J) > 0 > H(2s_1)$, because

$$r^* = \min_p \bar{r}(p) = 2 \min_p \bar{s}(p) = 2s_J \tag{5.68}$$

and analogously $r^{**} = 2s_1$. Part (iii) is shown and we now prove (i) and (ii).

Since we have no dominance, the only panmictic equilibria are the vertices $p_j = 1$ with $j = 1, \dots, J$ and it suffices to study their stability. We let $p_j \longrightarrow 1$ in (5.61) and due to

$$(r_i - \bar{r}) = (s_i - \bar{s}) \longrightarrow (s_i - s_j) \tag{5.69}$$

we get

$$\Delta p_i \sim p_i(s_i - s_j)H(2s_j) \tag{5.70}$$

for every $i, j \in \mathcal{J}$ with $i \neq j$.

We obtain from the strictly decreasing monotonance of H that $H(2s_1) < H(2s_2) < \cdots < H(2s_J)$, since $s_1 > s_2 > \cdots > s_J$. So $\Delta p_i < 0$ for every $i \neq 1$, which means that all the vertices $i \neq 1$ are unstable if $p_1 \sim 1$ and $H(2s_1) > 0$, because in that case $(s_i - s_1) < 0$ for every $i \neq 1$. Therefore, $p_1 = 1$ is asympotically stable if $H(2s_1) > 0$. Analogously, $\Delta p_i < 0$ for every $i \neq J$ if $p_J \sim 1$ and $H(2s_J) < 0$. Therefore, $p_J = 1$ is asympotically stable if $H(2s_J) < 0$. We see that the fixation of an intermediate allele $(1 < j < J)$ is always unstable and this completes the proof (cf. [3]). □

In Theorem 5.11 and 5.12 we assumed that J and K are arbitrary. Therefore, we can have an arbitrary number of alleles present in a stable not isolated equilibrium for any given K. We want to point out that this is also possible for no dominance as Theorem 5.12 shows.

If we assume multiplicity of the selection coefficients r_{ij}, there exist s_i, s_j such that we can write

$$r_{ij} = s_i s_j \tag{5.71}$$

and we have

$$r_i = s_i \bar{s}, \qquad \bar{r} = \bar{s}^2. \tag{5.72}$$

Nagylaki and Lou ([11], p. 312) showed that for multiplicity we even get the existence of a unique global attractor. This attractor can be specified similar to Theorem 5.12, but according to the case of multiplicative selection coefficients r_{ij}. The proof is akin to the proof of Theorem 5.12.

Instead of having arbitrarily many alleles at equilibrium, we now investigate under which circumstances an allele gets lost.

5.2.4 Loss of an Allele

In this subsection we present some general theorems about sufficient conditions for nonexistence of an internal equilibrium and for global loss of an allele. Further, we deduce information on which alleles will be lost. Therefore, we investigate the general mapping $\Delta_J \longrightarrow \Delta_J$ with

$$p_i^{'} = p_i f_i(p) \tag{5.73}$$

for every $i \in \mathcal{J}$, where $f_i(p) > 0$ for every $p \in \mathrm{int}\Delta_J$ and every $i \in \mathcal{J}$. Further

$$\sum_i p_i f_i(p) = 1 \tag{5.74}$$

for every $p \in \Delta_J$ and $f_i(p)$ is continuous for every $p \in \Delta_J$ and every $i \in \mathcal{J}$. By setting

$$f_i(p) = \sum_k c_k \frac{w_{i,k}(p)}{\bar{w}_k(p)} \tag{5.75}$$

we are able to apply all the following results to the Levene model.

We start with defining the support of a vector $a \in \Delta_J$ as

$$S_a = i \in \mathcal{J} : a_i > 0 \tag{5.76}$$

and we say that allele A_i is in S_a if $i \in S_a$. A sufficient condition for the nonexistence of an internal equilibrium is given by Nagylaki and Lou ([12], p. 403).

Theorem 5.13. *If there exist vectors $a \in \Delta_J$ and $b \in \Delta_J$ such that*

$$\sum_j a_j f_j(p) > \sum_j b_j f_j(p) \tag{5.77}$$

for every $p \in int\Delta_J$, then (5.73) has no internal equilibrium and there exist a and b such that $S_a \cap S_b = \varnothing$.

This theorem implies that if $p(t)$ converges as $t \longrightarrow \infty$, at least one allele must be eliminated, because there does not exist an internal equilibrium. In the Levene model, under the generic assumption that all the equilibria of (5.12) are isolated points, we have convergence of $p(t)$. Therefore, we know that in this case, under the assumption of (5.77), at least one allele will get lost.

The converse of the theorem does hold in some special cases of an ecological model and some game-theoretic scheme assumption on the fitness coefficients. In general, it is not determined, whether the converse holds, but it is supposed that it does not ([12], p. 404).

We now define

$$\hat{\Delta}_J(D) = \{p \in \Delta_J : p_j > 0 \quad \forall j \in D\} \tag{5.78}$$

for any set $D \subset \mathcal{J}$, so we can express that all the "‘favoured"’ alleles, i.e. those in S_a, are initially present and that (5.77) holds whenever all "‘deleterally"’ alleles, i.e. those in S_b, are present, by assuming that $p(0) \in \hat{\Delta}_J(S_a)$ and $p \in \hat{\Delta}_J(S_b)$. Nagylaki and Lou ([12], p. 403) proved the following theorem about the global loss of an allele.

Theorem 5.14. *If $p(0) \in \hat{\Delta}_J(S_a)$ and there exist $a \in \Delta_J$ and $b \in \Delta_J$ such that (5.77) holds for every $p \in \hat{\Delta}_J(S_b)$, and $p(t)$ converges as $t \longrightarrow \infty$, then $p_i(t) \longrightarrow 0$ as $t \longrightarrow \infty$ for some $i \in S_b$.*

Since in the Levene model we have generic convergence to isolated points, the assumption of congervence in Theorem 5.14 is unnecessary.

If we suppose that Theorem 5.14 holds on every surface of Δ_J with at least two alleles present, then Theorem 5.13 implies that the vertices are the only equilibria, since there can not exist an internal equilibrium. The vectors a and b may depend on the face of Δ_J. If $p(t)$ converges, we can say that one and only one of the vertices is globally asymptotically stable, because if there were two asymptotically stable vertices, then there would have to be at least one equilibrium on the edge that joins them. Since this is not the case due to Theorem 5.13, the unique aymptotically stable vertex is the global attractor ([12], p. 403).

If we suppose that the support of a equals i and we are satisfied with less detailed results, then we can delete the convergence assumption from Theorem 5.14. We set

$$\widetilde{\Delta}_J = \hat{\Delta}_J(i \cup S_b), \tag{5.79}$$

$$H_i(p) = \ln p_i - \sum_{j \in S_b} b_j \ln p_j \tag{5.80}$$

and

$$g = \prod_{j \in S_b} p_j. \tag{5.81}$$

We can now present a Theorem by Nagylaki and Lou ([12], p. 404), which gives us information on which alleles will get lost.

Theorem 5.15. *Suppose that $p(0) \in \widetilde{\Delta}_J$, and*

$$f_i(p) > \sum_{j \in S_b} b_j f_j(p) \tag{5.82}$$

for some $i \in \mathcal{J}$, *some* $b \in \Delta_J$ *and every* $p \in \widetilde{\Delta}_J$. *Then* $H_i(p)$ *is strictly increasing along orbits in* $\widetilde{\Delta}_J$ *and* $g(t) \longrightarrow 0$ *as* $t \longrightarrow \infty$.

We define $f_{ij} = f_j(e^{(i)})$ and get from (5.75) that

$$f_{ij} = \sum_k c_k \frac{w_{ij,k}}{w_{ii,k}}. \tag{5.83}$$

For the Levene model without dominance we get from (5.32) that

$$f_i(p) = \frac{1}{2}[1 + g_i(p)], \tag{5.84}$$

$$g_i(p) = \sum_k c_k \frac{v_{i,k}}{\bar{v}_k(p)}, \tag{5.85}$$

and therefore, the Theorems can be applied. Further (5.83) and (2.18) yield to

$$f_{ij}(p) = \frac{1}{2}(1 + g_{ij}), \tag{5.86}$$

$$g_{ij}(p) = \sum_k c_k \frac{v_{j,k}}{v_{i,k}}. \tag{5.87}$$

In order to give a condition for the loss, and later on also for the fixation of an allele, we assume for the homozygote fitnesses that

$$w_{ii,k} \geq w_{i+1,i+1;k} \tag{5.88}$$

for every $i \in \mathcal{J}_J$ and $k \in \mathcal{K}$, and also that

$$w_{11,l} > w_{JJ,l} \tag{5.89}$$

for some $l \in \mathcal{K}$. Thus, in every deme, allele A_1 and A_J are those with the greatest and smallest homozygote fitness, respectively. Further we suppose that

$$w_{1i,k} \geq w_{iJ,k} \tag{5.90}$$

for every $i \in \mathcal{J}$ and $k \in \mathcal{K}$, so that every heterozygote formed by A_1 is at least as fit as the corresponding heterozygote formed by A_J. Additionally, by setting $i = 1$ and $i = J$ in (5.90) we obtain

$$w_{11,k} \geq w_{1J,k} \geq w_{JJ,k} \tag{5.91}$$

for every $k \in \mathcal{K}$ and we see that in every deme allele A_1 and A_J are jointly neither underdominant nor overdominant.

We give a condition ([12], p. 406) for the loss of an allele.

Proposition 5.16. *If (5.89) and (5.90) hold, then* $p_J(t) \longrightarrow 0$ *as* $t \longrightarrow \infty$.

Proof. We suppose that the homozygote fitness of A_1 is greater than that of A_J. We do not say they have the greatest or smallest homozygote fitesses, but we suppose that in every niche they are jointly neither underdominant nor overdominant. Since in some niche k (5.90) holds, at least one of the inequalities in (5.91) must be strict. Consequently, for $k = l$ and $i = 1$, or $i = J$ also inequality (5.90) must be strict.

From (2.6) and the assumptions we infer that $w_{1,k}(p) > w_{J,k}(p)$ for every $p \in \widetilde{\Delta}_J(1, J)$ and from (5.75) that $f_1(p) > f_J(p)$. Applying Theorem 5.15 completes the prove. □

We pass on to the next subsection, which deals with conditions under which an allele gets fixed.

5.2.5 Fixation of an Allele

By using Propostion 5.16 iteratively, Nagylaki and Lou ([12], p. 406) showed the following condition for fixation of an allele.

Corollary 5.17. *Suppose (5.88) holds. If*

$$w_{11,l} > w_{22,l} \tag{5.92}$$

for some $l \in \mathcal{K}$ *and*

$$w_{1i,k} \geq w_{ij,k} \tag{5.93}$$

for every $i, j \in \mathcal{J}$ *such that* $i \leq j$ *and for every* $k \in \mathcal{K}$*, then* $p_1(t) \longrightarrow 1$ *as* $t \longrightarrow \infty$*.*

Proof. Since we assume that (5.88) holds, assumption (5.92) implies (5.89) and by setting $j = J$ in (5.93), we see that also (5.90) holds. We can therefore apply Proposition 5.16, which implies that allele J will be lost as $t \longrightarrow \infty$. We now consider only alleles $A_1, A_2, \ldots, A_{J-1}$. Proposition 5.16 yields $p_{J-1}(t) \longrightarrow 0$ as $t \longrightarrow \infty$. Iterating this argument eventually leads to $p_1(t) \longrightarrow 1$ as $t \longrightarrow \infty$. ☐

So under the assumption of Corollary 5.17 the allele with the strictly greatest homozygote fitness in every deme will be ultimately fixed.

We now present a special case of assumptions (5.88) and (5.90), which is the complete absence of underdominance and overdominance in every deme. In that case we get

$$w_{ii,k} \geq w_{ij,k} \geq w_{jj,k} \tag{5.94}$$

for every $i, j \in \mathcal{J}$ such that $i < j$ and every $k \in \mathcal{K}$. Indeed, by setting $i = 1$ and then $j = J$ we see that (5.94) yields

$$w_{1i,k} \geq w_{ii,k} \geq w_{iJ,k} \tag{5.95}$$

for every $i \in \mathcal{J}$ and $k \in \mathcal{K}$. Since this is a special case of (5.88) and (5.90), obviously if (5.94) holds, so do (5.88) and (5.90). We obtain the following Proposition:

Proposition 5.18. *Suppose (5.94) holds, then (5.92) implies that* $p_1(t) \longrightarrow 1$ *and* $t \longrightarrow \infty$*.*

Proof. Since (5.94) holds, by using (5.95) it follows that (5.92) in Corollary 5.17 holds and, thus, the corollary can be applied.

So if in every deme the homozygotes have the same fitness order and both underdominance and overdominance are absent, then the allele with the strictly greatest homozygote fitness in every deme gets ultimately fixed. ☐

We now state that proposition (3.4) for fixation of an allele in the general selection-migartion model is valid also for the Levene model ([12], p. 406).

Proposition 5.19. *Proposition (3.4) also applies to the Levene model.*

If there is no dominance, the following Proposition by Nagylaki and Lou ([12], p. 407) gives a sufficient condition for global fixation of a specific allele.

Proposition 5.20. *If there exists some $i \in \mathcal{J}$, such that*

$$g_{ij} = \sum_k c_k \frac{v_{j,k}}{v_{i,k}} < 1 \tag{5.96}$$

for every $j \in \mathcal{J}$, then $p_i(t) \longrightarrow 1$ as $t \longrightarrow \infty$.

Proof. We need to show that vertex i is asymptotically stable along the ij-edge for every $j \in \mathcal{J}_i$. So the problem reduces to the diallelic case. Consider two alleles A and a, with the allelic frequencies p and $q = 1 - p$. For further properties recall Subsection 5.3.2. In order for A to be fixed, $p = (1, \ldots, 1)$ needs to be stable, which is the case if and only if a is not protected. So we will see from (5.106) that therefore, the condition

$$\sum_k \frac{c_k}{u_k} < 1 \tag{5.97}$$

needs to be fulfilled. Inserting for u_k and identifying $A = A_i$ and $a = A_j$ leads to

$$f_{ij} = \sum_k c_k \frac{w_{ij,k}}{w_{ii,k}} < 1 \tag{5.98}$$

which is identical to (5.83). If (5.98) holds for every $j \in \mathcal{J}_i$, than vertex i is asymptotically stable. Without dominance, by inserting (2.18) into (5.98) we get

$$\begin{aligned}
\sum_k c_k \frac{v_{i,k} + v_{j,k}}{2v_{i,k}} &< 1 \\
\frac{1}{2} \sum_k c_k \left(1 + \frac{v_{j,k}}{v_{i,k}}\right) &< 1 \\
1 + \sum_k c_k \frac{v_{j,k}}{v_{i,k}} &< 2 \\
\sum_k c_k \frac{v_{j,k}}{v_{i,k}} &< 1, \qquad (5.99)
\end{aligned}$$

which is g_{ij} in (5.87). By Theorem 5.7 and 5.5 the asymptotical stability of vertex i is global. ☐

5.3 Two Alleles

In this section we investigate the Levene model with two alleles A and a. We want to point out that at the end of Subsection 5.2.1 we already presented a condition for the diallelic case under which there exists exactly one stable, globally attracting equilibrium.

Due to Corollary 5.4 we can show the following substantial corollary:

Corollary 5.21. *If there are two alleles and a protected polymorphism, then all trajectories converge to some stable internal equilibrium point (no manifold).*

Proof. In the diallelic case, the simplex is the interval $[0, 1]$. Together with the result of Corollary 5.4, we can conclude that every trajectory converges to an equilibrium point. ☐

5.3.1 Formulation

The transformation equation which models the transition from one generation to its successive, is given by

$$p_{i,k}^{'} = \sum_l m_{kl} f_l(p_{i,l}), \tag{5.100}$$

for every $i \in \mathcal{J}$ and every $k, l \in \mathcal{K}$, where $f_l(p_{i,l})$ denotes the selection function in deme l defined below. This transformation relation for the Levene model derives from our general selection-migration dynamics (2.9).

Following our notation from Section 3.1 for the general selection-migration model, we denote the viability parameters of the genotypes as shown in Table 3.1 for every $k \in \mathcal{K}$ and $0 < u_k, v_k < \infty$. It suffices to observe $p_k = p_{i,k}$, since we have only two alleles and $p_{2,k} = 1 - p_{1,k}$. Furthermore, we know that in the Levene model after one generation of migration the allele frequencies are equal in every niche (5.6), thus, the system can now be expressed in terms of a single variable p. By consulting the selection dynamics (2.8), the selection function in deme k is

$$f_k(p) = p\frac{w_{1,k}}{\bar{w}_k} = \frac{u_k p^2 + p(1-p)}{u_k p^2 + 2p(1-p) + v_k(1-p)^2}. \tag{5.101}$$

Therefore, the Levene dynamics with soft selection and two alleles can be written as

$$p^{'} = \sum_k c_k f_k(p) = f(p). \tag{5.102}$$

Due to this natural simplification of the dynamics, many results can be obtained.

5.3.2 Protected Polymorphism

In concordance with Section 3.1, for A being protected from extinction, we need the dominant eigenvalue of the Jacobian of the entire dynamics

$$Q = MD, \qquad Q = (q_{kl}) \tag{5.103}$$

at $p = (0, \ldots, 0)$, with

$$q_{kl} = \frac{m_{kl}}{v_l} = \frac{c_l}{v_l}. \tag{5.104}$$

The fitness values are given in Table 3.1. Since q_{kl} is independent of k, all the row sums are identical and we get equality in (3.3). The maximal eigenvalue can therefore be computed by

$$\lambda_0 = \sum_l \frac{c_l}{v_l}. \tag{5.105}$$

Secton 3.1 tells us that A is protected from loss, that means $p = 0$ is unstable if

$$\lambda_0 > 1 \tag{5.106}$$

or if the harmonic mean of the fitnesses v_k is less then 1 ([10], p. 149). That is

$$\tilde{v} := \left(\sum_l \frac{c_l}{v_l}\right)^{-1} < 1 \tag{5.107}$$

with $\tilde{v}$ being the weighted harmonic mean of the v_l.

Analogously, a is protected or equivalently $p = 1$ is unstable if

$$\tilde{u} := \left(\sum_l \frac{c_l}{u_l} \right)^{-1} < 1. \tag{5.108}$$

If A is recessive, thus, $v_l = 1$ for every $l \in \mathcal{K}$, we see that $\lambda_0 = 1$ and the above criterium can not be applied. Observing that c is the maximal left eigenvector of M we find that A is protected if the arithmetic mean of the fitness ratios u_l exceed unity

$$\bar{u} = \sum_k c_k u_k > 1. \tag{5.109}$$

From (5.108) and (5.109) we get that a sufficient condition for a protected polymorphism is in this case ([10], p. 150),

$$u^* < 1 < \bar{u}. \tag{5.110}$$

In the special case of two niches, we obtain from Bulmer ([4], p. 256-257) and Bürger's lecture notes [3] a necessary condition for a protected polymorphism.

Lemma 5.22. *We suppose two niches and assume without loss of generality that* $v_1 > 1$ *and* $v_2 < 1$*. Analogously, we suppose without loss of generality that* $u_1 > 1$ *and* $u_2 < 1$*. Then there exists a protected polymorphism if*

$$\frac{c_1}{1 - v_2} + \frac{c_2}{1 - v_1} < 1 \qquad (A \text{ is protected}) \tag{5.111}$$

and

$$\frac{c_1}{1 - u_2} + \frac{c_2}{1 - u_1} < 1 \qquad (a \text{ is protected}). \tag{5.112}$$

For the case of equality in (5.111) or (5.112), we do not derive implications on the existence of a protected polymorphism. Thus, we obtain only the sufficient condition in Lemma 5.22.

Under the absence of dominance, the following equivalence for the existence of an internal, globally stable equilibrium, and consequently for the existence of a protected polymorphism, holds:

Lemma 5.23. *Suppose two niches and no dominance, thus* $u_k + v_k = 2$*. Then there exists a globally stable internal equilibrium if and only if*

$$|\kappa| < 1, \tag{5.113}$$

where

$$\kappa = \frac{c_1}{1 - v_2} + \frac{c_2}{1 - v_1}. \tag{5.114}$$

Proof. From $u_k + v_k = 2$, we get $u_k = 2 - v_k$. Inserting this in Lemma 5.22 leads to

$$\begin{aligned} \frac{c_1}{1 - (2 - v_2)} + \frac{c_2}{1 - (2 - v_1)} &< 1 \\ \frac{c_1}{-1 + v_2} + \frac{c_2}{-1 + v_1} &< 1 \\ \frac{c_1}{1 - v_2} + \frac{c_2}{1 - v_1} &> -1 \end{aligned} \tag{5.115}$$

and consequently to

$$\left|\frac{c_1}{1-v_2}+\frac{c_2}{1-v_1}\right|<1. \tag{5.116}$$

□

We refer to Section 5.4 for further investigations and numerical analysis on the existence of a protected polymorphism under various assumptions on the number of alleles, the number of niches and the type of dominance.

5.3.3 The Number of Possible Equilibria

The equilibrium states of the dynamics (5.102) are the solutions of the equation $p = f(p)$ with $0 \leq p \leq 1$ and we infer immediately that the two trivial equilibria are the fixation states $p = 0$ and $p = 1$. By using (5.106) we can say about their local stability that A is protected if

$$f^{'}(0)=\sum_k \frac{c_k}{v_k}>1 \tag{5.117}$$

and a is protected if

$$f^{'}(1)=\sum_k \frac{c_k}{u_k}>1. \tag{5.118}$$

Equivalently, we can say, as it follows also from intuition, that A is protected if $v_k \leq 1$ for every $k \in \mathcal{K}$ and there exists at least one $k \in \mathcal{K}$ such that $v_k < 1$. Alleles A is not protected if $v_k \geq 1$ for every $k \in \mathcal{K}$ and there exists at least one $k \in \mathcal{K}$ such that $v_k > 1$. Similarily, we get the corresponding results for a.

The case when the fitness values v_k are greater 1 in some niches and smaller 1 in others and analogously for u_k, was investigated for the case of two niches in the preceeding subsection. Thus, for the case of two alleles and two niches, we know what happens either way.

In order to find the possible polymorphic equilibrium frequencies in the Levene model with two alleles, we obtain by a series of simple calculations:

$$\begin{aligned}
&f(p)-p=0 \qquad\qquad (5.119)\\
&\frac{f(p)}{p}-1=0\\
&\sum_k c_k\frac{u_kp+1-p}{u_kp^2+sp(1-p)+v_k(1-p)^2}-\sum_k c_k=0\\
&\sum_k c_k[\frac{u_kp+1-p}{u_kp^2+sp(1-p)+v_k(1-p)^2}-1]=0\\
&(1-p)\sum_k c_k\frac{p(u_k+v_k-2)+1-v_k}{u_kp^2+sp(1-p)+v_k(1-p)^2}=0. \qquad (5.120)
\end{aligned}$$

By setting

$$g(p)=\sum_k c_k\frac{p(u_k+v_k-2)+1-v_k}{u_kp^2+sp(1-p)+v_k(1-p)^2} \tag{5.121}$$

the equation $p = f(p)$ reduces to

$$p(1 - p)g(p) = 0. \tag{5.122}$$

Obviously, $g(p)$ is a rational function. By converting the summands to an equal denominator and multiplying by it, we see that the zeros of $g(x)$ are those of a polynomial $P(x)$ of degree $2K - 1$. This is an upper bound on the number of possible polymorphisms. Together with the two fixation states $p = 0$ and $p = 1$, we have $2K + 1$ equilibria of which K or $K + 1$ are stable.

Therefore, in the case of two niches, generally, there can be at most three internal equilibrium points, independent of the choice of the fitness values. Plotting p against $p^{'} = f(p)$, we see that every intersection of the curve $f(p)$ with the diagonal $p = p^{'}$ represents an equilibrium point of the dynamics (5.102). If we assume that there exists a protected polymorphism, condition (5.117) and (5.118) concerning the slop of $f(p)$ in $p = 0$ and $p = 1$ need to hold. Thus, the equilibria at the boundaries always need to be unstable in order for a protected polymorphism to exist. Consequently, only two cases of equilibrium configurations are possible and illustrated in Figure 5.2 and 5.3: The existence of a unique stable internal equilibrium or the existence of three internal equilibrium points, of which two not neighboring ones are stable and the one in between is unstable.

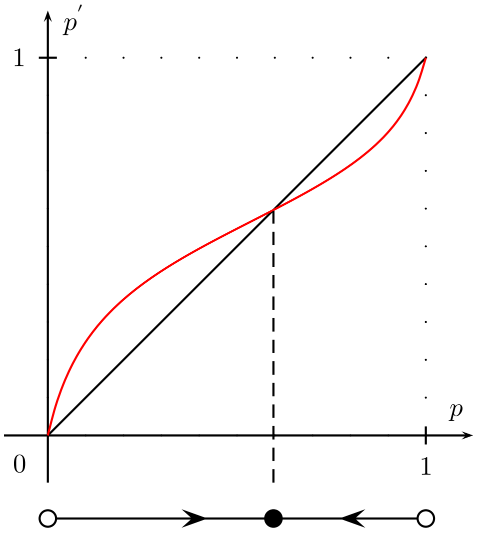

Fig. 5.2: Protected polymorphism with a unique stable internal equilibrium

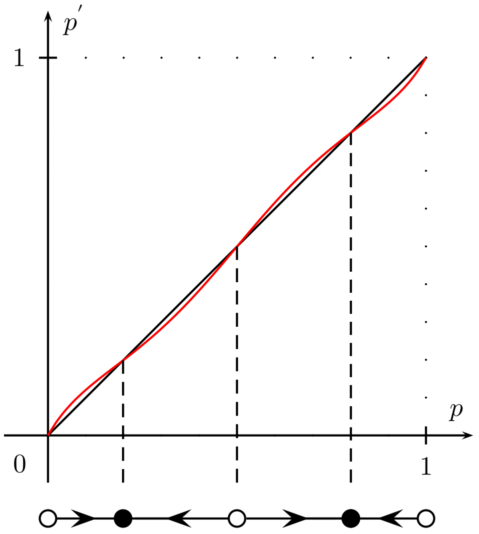

Fig. 5.3: Protected polymorphism with three internal equilibrium points

Table 5.1 shows the parameters used to plot Figure 5.2. The fitness values entail a unique stable internal equilibrium at $p = 0.59684$. In Table 5.2, we see fitness values that generate three interal equilibrium points. The two stable ones are at $p = 0.19864$ and $p = 0.80136$, and the unstable one is at $p = 0.5$, as can be seen in Figure 5.3.

Genotypes	AA	Aa	aa
Niche 1	6.69024	1	0.11626
Niche 2	0.13196	1	2.98791

Table 5.1: Fitnesses for a protected polymorphism with a unique stable internal equilibrium (see Figure 5.2)

Genotypes	AA	Aa	aa
Niche 1	33.75	1	33.75
Niche 2	0.28254	1	0.28254

Table 5.2: Fitnesses for a protected polymorphism with three internal equilibrium points (see Figure 5.3)

5.3.4 Maximum Number of Polymophic Equilibrium Points

Now we present four Theorems that specify the numbers of polymorphic equilibrium points under certain configurations of the selection parameters. We start with a sufficient condition deduced from Lemma 5.8 and Theorem 5.5 that guarantees at most one polymorphic equilibrium. If it exists, it is globally stable (cf. [3]).

Theorem 5.24. *If* $u_k v_k \leq 1 + (1 - v_k)^2$ *and* $v_k \leq 1$*, or* $u_k v_k \leq 1 + (1 - u_k)^2$ *and* $u_k \leq 1$ *for every* $k \in \mathcal{K}$*, then there exists at most one internal equilibrium state. If an equilibrium point (it does not matter whether it is internal or on the boundary) is locally stable, then it is globally stable. Thus, when a polymorphism is present, this state is globally stable and the two fixation states are unstable.*

Proof. We obtain from Lemma 5.8 that $F(p)$ is concave and consequently, Theorem 5.5 can be applied. Thus, there exists exactly one stable equilibrium (point or manifold) and it is globally attracting. Consequently, every locally stable equilibrium is globally stable. Further, Theorem 5.5 states that if there exists an internal equilibrium, it is the global attractor. Therefore, there can exist at most one polymorphic equilibrium which is globally stable if it exists. ☐

Only three configurations of equilibria are possible under the assumptions of Theorem 5.24 which are shown schematically in Figure 5.4.

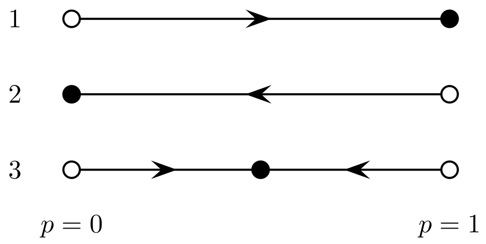

Fig. 5.4: Schematical equilibrium configurations

Karlin ([7], p. 378-379) proved the statements of Theorem 5.24 for the slightly weaker assumption of submultiplicative fitness values of u_k and v_k, thus $u_k v_k \leq 1$ for every $k \in \mathcal{K}$. Submultiplicative fitness is in force and therefore Theorem 5.24 can be applied, for instance, in the following cases:

- There is overdominance in every niche, thus, $u_k < 1$ and $v_k < 1$ in Table 3.1 for every $k \in \mathcal{K}$. In this situation both fixation states are unstable and a unique globally stable polymorphism is generated as shown by case three in Figure 5.4.

- We have directed selection in every deme due to additivity. Then the fitness values have the form as shown in Table 5.3 with $|s_k| \leq 1$ for every $k \in \mathcal{K}$.

Genotypes	AA	Aa	aa
Relative Fitness Values	$1 + s_k$	1	$1 - s_k$

Table 5.3: Relative fitness values for additivity

Therefore, $u_k v_k = 1 - s_k^2 < 1$.

- If we have multiplicative allelic effects. The corresponding fitness coefficients are shown in Table 5.4 and clearly we have $u_k v_k = 1$.

Genotypes	AA	Aa	aa
Relative Fitness Values	γ_k	1	$\frac{1}{\gamma_k}$

Table 5.4: Relative fitness values for multiplicity

- A haploid population in the Levene model with a selection regime as in Table 5.5 and the corresponding viability function

$$f_k(p) = \frac{u_k p}{u_k p + v_k(1-p)} \tag{5.123}$$

has the same evolution as a diploid viability scheme with multiplicative fitness, setting $\gamma_k = \frac{u_k}{v_k}$. Therefore, in the Levene model with a haploid locus, at most one polymorphic equilibrium is established.

Genotypes	A	a
Relative Fitness Values	u_k	v_k

Table 5.5: Relative fitness values in the haploid case

We now present a sufficient condition for the existence of a unique unstable internal equilibrium as it is shown schemtically in Figure 5.4. The proof can be found in Karlin ([7], p. 379).

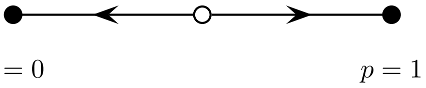

Fig. 5.5: Schematical delineation of a unique unstable internal equilibrium

Theorem 5.25. *Suppose that $u_k v_k > 1$ such that*

$$u_k v_k > 1 + \max\left\{(u_k - 1)^2, (v_k - 1)^2\right\} \tag{5.124}$$

for every $k \in \mathcal{K}$ and assume that at least one polymorphism exists. Then both fixation states are stable and a unique internal unstable equilibrium is generated.

We now examine the properties of the selection regime shown in Table 5.6 with

Genotypes	AA	Aa	aa
Relative Fitness Values	$1 + s_k$	$1 + hs_k$	$1 - s_k$

Table 5.6: Relative fitness values for equal relative dominance

$|s_k| \leq 1$. Since h is independent of the deme, we have the same degree of dominance to allele a in every niche. If $|h| \leq 1$, the heterozygote has an intermediate fitness value between the two homozygotes in every deme. Allele A is dominat if $h = 1$ and recessive if $h = -1$. If $h = 0$ we have additive fitness. Moreover, when $h > 1, s_k > 0$, there is overdominance in niche k, when $h < 1, s_k > 0$ we have local underdominance. Since the heterozygote fitness can not be ≤ 0, h is constrained to satisfy $h > -\frac{1}{s_k}$ if $s_k > 0$ and $h < -\frac{1}{s_k}$ if $s_k < 0$. Theorem 5.24 can not be applied to the fitness scheme of Table 5.6, but the following Theorem ([7], p. 368) describes the possible outcomes.

Theorem 5.26. *(i) Suppose the selection regime of Table 5.6 is in force, then there exist at most two internal equilibria. When two internal equilibria exist, one of the fixation states and one of the polymorphisms are simultaneously stable.*

(ii) With complete dominance, which is the case of the selection regime in Table 5.6 if $|h| \leq 1$, at most one single internal equilibrium exists and if it is present, it is globally stable.

Proof. We insert the fitness values of Table 5.6 in (5.121).

$$\begin{aligned} g(p) &= \sum_k c_k \frac{p\frac{1+s_k}{1+hs_k} + p\frac{1-s_k}{1+hs_k} - 2p + 1 - \frac{1-s_k}{1+hs_k}}{\frac{1+s_k}{1+hs_k}p^2 + 2p(1-p) + \frac{1-s_k}{1+hs_k}(1-p)^2} \\ &= \sum_k c_k \frac{p(1+s_k) + p(1-s_k) - 2p(1+hs_k) + 1 + hs_k - 1 + s_k}{(1+s_k)p^2 + 2p(1-p)(1+hs_k) + (1-s_k)(1-p)^2} \\ &= \sum_k c_k \frac{-2phs_k + hs_k + s_k}{2phs_k - 2p^2hs_k + 1 - s_k + 2ps_k} \\ &= (1 + h(1-2p)) \sum_k \frac{c_k s_k}{1 + s_k(2p - 1 + 2hp(1-p))}, \end{aligned} \tag{5.125}$$

For a polymorphic equilibrium to exist, either the sum or the factor $1 + h(1 - 2p)$, which is independent of s_k, need to equal 0. By setting the factor $1 + h(1 - 2p) = 0$ we obtain the equilibrium point

$$\hat{p} = \frac{1 + h}{2h} \tag{5.126}$$

which leads to a relevant output of $\hat{p} \in (0, 1)$ if and only if $|h| > 1$. For $h > 1$, $\hat{p}$ is stable (unstable) provided

$$\sum_k \frac{c_k s_k}{1 + s_k \frac{h^2+1}{2h}} > 0 \qquad (< 0). \tag{5.127}$$

For $h < -1$ these inequalities are reversed.

Let us consider $\varphi(p) = 2p - 1 + 2hp(1 - p)$, then $\varphi(0) = -1$ and $\varphi(1) = 1$. Further, for $|h| \leq 1$, φ is strictly monotone in $[0, 1]$. We now consider

$$P(x) = \sum_k \frac{c_k}{\frac{1}{s_k} + x} \tag{5.128}$$

with $x \in [-1, 1]$. Then obviously,

$$P^{'}(x) = -\sum_k \frac{c_k}{(\frac{1}{s_k} + x)^2} < 0 \tag{5.129}$$

and since $|\frac{1}{s_k}| > 1$ and $|x| \leq 1$ for $|h| \leq 1$, the function $P(x)$ is defined in the entire interval $[-1, 1]$. Therefore, for $|h| \leq 1$ there can be at most one zero in $(0, 1)$. Since $\varphi(p)$ is strictly monotone, also

$$\sum_k \frac{c_k s_k}{1 + s_k \varphi(p)} \tag{5.130}$$

has at most one zero in $(0, 1)$. As a result, for $|h| \leq 1$ in total, there can be at most one zero in $(0, 1)$ and consequently, just one internal equilibrium.

For $|h| > 1$, φ has a maximum or minimum in $(0, 1)$ and the sum in (5.125) can produce at most 2 zeros in $[0, 1]$. ☐

For local directed selection forces in every deme, Karlin ([7], p. 366) stated the following principle.

Principle 5.27. *With a mosaic of directed selection, there can exist at most one stable polymorphic equilibrium.*

Following Karlin, a principle is valid for a large spectrum of examples, but there can be extreme cases in which it does not hold. For instance, if we have directed selection in every niche, it can happen that there are three stable equilibria, the two fixation states and an internal equilibrium, whereas in the case of additivity, multiplicity or a dominant trait this can not occur.

We now study a selection pattern with underdominance or overdominance in each deme. We assume that the homozygotes have the same fitness values, thus, $u_k = v_k$ for every $k \in \mathcal{K}$. The selection regime is given in Table 5.7, where $u_k < 1$ implies

Genotypes	AA	Aa	aa
Relative Fitness Values	u_k	1	u_k

Table 5.7: Relative fitness values for underdominance or overdominance

overdominance in deme k, whereas $u_k > 1$ describes underdominance. By inserting $p = \frac{1}{2}$ in (5.121), we see that the polymorphic equilibrium $p^* = \frac{1}{2}$ always exists:

$$\begin{aligned}
g(p) &= \sum_k c_k \frac{p(2u_k - 2) + 1 - u_k}{u_k p^2 + 2p(1-p) + u_k(1-p)^2}, \\
g(\frac{1}{2}) &= \sum_k c_k \frac{u_k - 1 + 1 - u_k}{\frac{1}{2}u_k + \frac{1}{2}} = 0. \qquad (5.131)
\end{aligned}$$

In order to investigate its stability, we need to calculate $f^{'}(\frac{1}{2})$. We start by differentiating $f(p)$:

$$\begin{aligned}
f(p) &= \sum_k c_k \frac{u_k p^2 + p(1-p)}{u_k p^2 + 2p(1-p) + u_k(1-p)^2}, \\
f^{'}(p) &= \sum_k c_k \left[\frac{(2u_k p + 1 - 2p)(u_k p^2 + 2p - 2p^2 + u_k - 2pu_k + u_k p^2)}{[u_k p^2 + 2p(1-p) + u_k(1-p)^2]^2} \right. \\
&\qquad \left. - \frac{(u_k p^2 + p - p^2)(2u_k p + 2 - 4p - 2u_k + 2u_k p)}{[u_k p^2 + 2p(1-p) + u_k(1-p)^2]^2} \right] \\
&= \sum_k c_k \frac{2u_k^2 p - 2u_k^2 p^2 + u_k - 2pu_k + 2u_k p^2}{[u_k p^2 + 2p(1-p) + u_k(1-p)^2]^2} \\
&= \sum_k c_k \frac{u_k(2u_k p - 2u_k p^2 + 1 - 2p + 2p^2)}{[u_k p^2 + 2p(1-p) + u_k(1-p)^2]^2} \qquad (5.132)
\end{aligned}$$

Now inserting the equilibrium $p^* = \frac{1}{2}$ leads to

$$\begin{aligned}
f^{'}(\frac{1}{2}) &= \sum_k c_k \frac{u_k(u_k - \frac{1}{2}u_k + 1 - 1 + \frac{1}{2})}{(\frac{1}{4}u_k + \frac{1}{2} + \frac{1}{4}u_k)^2} \\
&= \sum_k c_k \frac{u_k \frac{1}{2}(u_k + 1)}{(\frac{1}{2}(u_k + 1))^2} \\
&= 2\sum_k c_k \frac{u_k}{1 + u_k}. \qquad (5.133)
\end{aligned}$$

Thus, we obtain from Subsection 5.3.2 that the equilibrium is stable if

$$f^{'}(\frac{1}{2}) < 1 \qquad (5.134)$$

and unstable if the reverse inequality holds. According to (5.106), the fixation states of allele A and symmetrically of allele a are stable if

$$f^{'}(0) = f^{'}(1) = \sum_k \frac{c_k}{u_k} < 1 \qquad (5.135)$$

and unstable if the reverse inequality holds.

The following description of the equilibrium configurations can be found in Karlin ([7], p. 368).

Theorem 5.28. *Suppose the selection regime shown in Table 5.7 holds, then at most three polymorphic equilibria exist. The characterization of the equilibira is the following:*

- *(i) If both fixation states are simultaneously stable, then they are the only locally stable equilibria. Consequently, the equilibrium $p^* = \frac{1}{2}$ is the unique internal equilibrium and needs to be unstable.*
- *(ii) If $p^* = \frac{1}{2}$ is stable, then it is the unique internal globally stable equilibrium. Thus, both the fixation states are unstable.*
- *(iii) If both fixation states and $p^* = \frac{1}{2}$ are unstable, then there exist two stable polymorphic equilibria $\bar{p}$ and $\bar{\bar{p}} = 1 - \bar{p}$ with $0 < \bar{p} < \frac{1}{2} < \bar{\bar{p}} < 1$, such that $\bar{p}$ is approached from any initial state p_0 with $0 < p_0 < \frac{1}{2}$ and $\bar{\bar{p}}$ is reached from any p_0 with $\frac{1}{2} < p_0 < 1$.*

  The points $\bar{p}$ and $\bar{\bar{p}}$ can be calculated as the values fulfilling $p(1-p) = \hat{z}$, where $\hat{z}$ is the unique solution in $0 < z < \frac{1}{4}$ of the equation

$$\sum_k \frac{c_k(1-u_k)}{u_k + 2(1-u_k)z} = 0. \tag{5.136}$$

The equilibrium configurations resulting from $(i) - (iii)$ of Theorem 5.28 are depicted schematically in Figure 5.6. From (5.134) and (5.135) we derive the areas of the

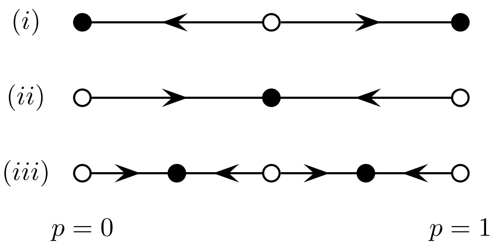

Fig. 5.6: Equilibrium configurations if $u_k = v_k$ in every niche

parameters u_1 and u_2 that entail the equilibrium configurations according to $(i) - (iii)$. For two niches of equal size, thus, $c_1 = c_2 = \frac{1}{2}$, we obtain from (5.134) that the boundary is given by

$$\frac{u_1}{1+u_1} + \frac{u_2}{1+u_2} = 1, \tag{5.137}$$

i.e.,

$$u_2 = \frac{1}{u_1}. \tag{5.138}$$

From (5.135) we obtain the boundary curve

$$u_2 = \frac{u_1}{2u_1 - 1}. \tag{5.139}$$

As illustrated in Figure 5.7, these two curves divide the u_1u_2 plane into regions of different equilibrium configurations. Area I denotes the region of parameter combinations where $p^* = \frac{1}{2}$ is the unique globally stable equilibrium point, thus, it corresponds to (i). Analogously, the regions II and III correspond to (ii) and (iii), respectively.

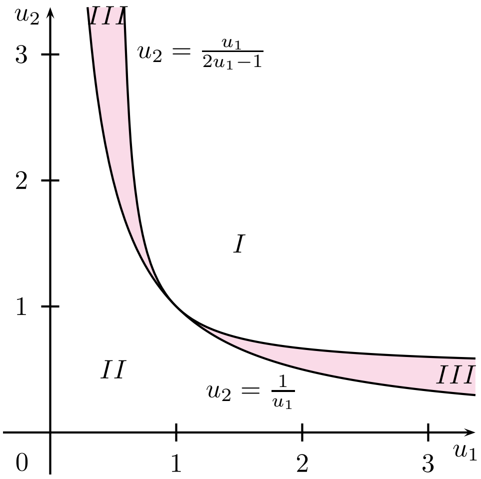

Fig. 5.7: Regions of equilibrium configurations as discussed in the main text.

5.4 Examples

At first, we address the issue of how big the parameter space is such that a protected polymorphism occurs in a population with two alleles. Distinguishing between no dominance and intermediate dominance, we study this problem analytically and numerically for the case of two demes. Provided no dominance, we extend our numerical analysis to three niches and four niches, respectively.

Afterwards, we assume that initially three alleles are present in the population. We investigate numerically how big the parameter space is such that a stable equilibrium with one, two, or three alleles, respectively, occurs. We will treat these cases under the assumption that there is no dominance for two, three and four niches, respectively.

5.4.1 Two Alleles and Two Demes

We consider the case of two alleles and two niches. By applying Lemma 5.23 and Lemma 5.22 from Section 5.3, we will illustrate the areas of parameter combinations that lead to a protected polymorphism. We will treat the cases of no dominance, as done in Nagylaki ([10], p. 148-151), and of intermediate dominance. Thus, we look for parameter combinations such that none of the two alleles A and a, can get fixed or lost.

For intermediate dominance, we investigate how the fraction of the parameter space changes that maintains a protected polymorphism, as the set of admissible parameters increases, and whether it is finite or not.

No Dominance

We assume no dominance, hence Theorem 5.24 holds, which tells us that there exists at most one polymorphic equilibrium, which is stable if it exists. In Figure 5.4 the first three cases illustrate which equilibrium configurations can occur. The genotypes of the two alleles A and a shall have the parametrisation given in Table 5.8 with

Genotypes	AA	Aa	aa
Relative Fitness Values	$1+s_k$	1	$1-s_k$

Table 5.8: Relative fitness values if there is no dominance

$s_k \in [-1,1)$, as it is also used by Nagylaki and Lou ([14], p. 130-132). Here, we prefer this parametrisation to our usual one, which is shown in Table 5.9 for the case of no dominance, and $v_k \in (0,2]$. The reason can be seen in Figures 5.10 and 5.11, and is

Genotypes	AA	Aa	aa
Relative Fitness Values	$2-v_k$	1	v_k

Table 5.9: Relative fitness values if there is no dominance, thus $u_k + v_k = 2$

simply that our graphics get shifted to the orgin, which makes it easier to calculate and analyse. We now explain how we derived that illustration and what it shows.

We suppose without loss of generality that our niche proportions are the same, thus, $c_1 = c_2 = \frac{1}{2}$. According to Lemma 5.23, Figure 5.8 shows the region of protection of allele A, which is given by

$$\frac{1}{s_2} + \frac{1}{s_1} < 2 \tag{5.140}$$

and which we denote by Π_1. We assume without loss of generality that $s_1 > 0$, since $s_1 < 0$ can be investigated analogously. Further, we know that A is protected if s_1 and s_2 are both greater than zero. Thus, it is left to distinguish two different cases to identify the regions of protection of allele A:

(i) $s_1 \in (0, \frac{1}{2}) \Rightarrow 0 > s_2 > \frac{s_1}{2s_1-1} > -1 \Rightarrow s_2 \in [\frac{s_1}{2s_1-1}, 0]$

(ii) $s_1 \in (\frac{1}{2}, 1] \Rightarrow \frac{s_1}{2s_1-1} > 0 > s_2 > -1 \Rightarrow s_2 \in [-1, 0]$

The boundary curve that designates the passage from loss of allele A to its protection, obviously, is

$$\frac{1}{s_2} + \frac{1}{s_1} = 2,$$

or

$$s_2 = \frac{s_1}{2s_1 - 1}. \tag{5.141}$$

We obtain that allele A is protected if either Aa is fitter than aa in both demes, thus, $s_k > 0$ for every $k \in \mathcal{K}$, or if Aa is fitter in one deme, less fit in the other, thus, $s_1 s_2 < 0$, and additionally (5.140) is fulfilled.

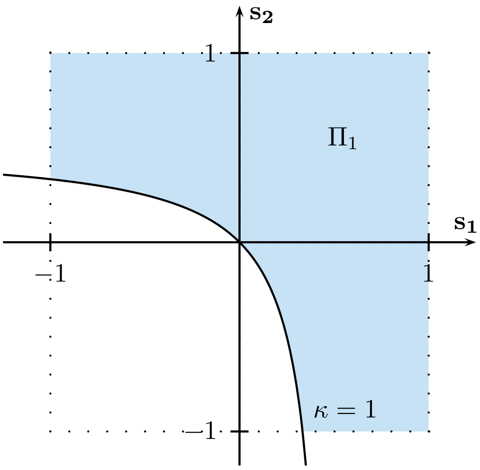

Fig. 5.8: Π_1 is the region of protection of allele A.

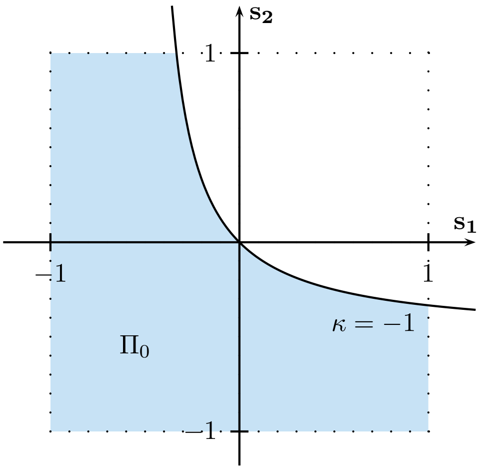

Fig. 5.9: Π_0 is the region of protection of allele a.

The region of protection of allele a under no dominance, with $s_k \in [-1, 1)$, is

$$\frac{1}{s_2} + \frac{1}{s_1} > -2, \tag{5.142}$$

as follows from Lemma 5.23. Analogously, the distinction of cases leads to the region of protection of allele a, which we denote by Π_0 and which is illustrated in Figure 5.9. The boundary curve is

$$\frac{1}{s_2} + \frac{1}{s_1} = -2,$$

or

$$s_2 = \frac{s_1}{-2s_1 - 1}. \tag{5.143}$$

In order to obtain a protected polymorphism both alleles need to be protected at the same time and thus,

$$\left| \frac{1}{s_2} + \frac{1}{s_1} \right| < 2. \tag{5.144}$$

Consequently, for protection of both alleles A and a, selection needs to act in the opposite direction in the two demes, thus, $s_k > 0$ in one deme and $s_k < 0$ in the other, and it must be sufficiently strong relative to migration, since (5.144) needs to hold. The corresponding illustration can be seen in Figure 5.10, where the light blue color marks the regions of protection of only one allele, and the dark blue color indicates Σ, the region of protected polymorphisms. We want to point out that Figure 5.10 is a composition of Figures 5.8 and 5.9.

As mentioned previously, under our usual parametrisation as shown in Table 5.9, the two curves would be reversed and they would intersect in $(1, 1)$. Thus, also the regions of protection would be reversed, as can be observed in Figure 5.11, for direct comparison.

We are now interested in how big the region of joint protection is. We use partial integration and integration by substitution to first calculate the volume of Λ (see

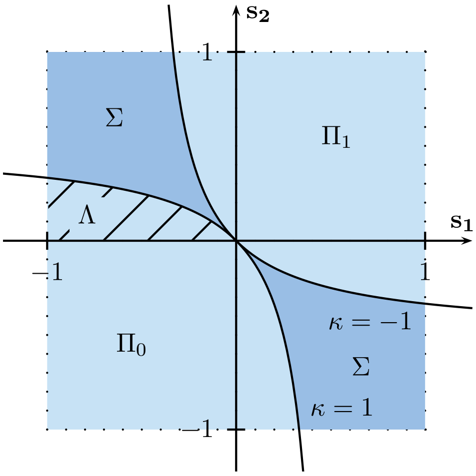

Fig. 5.10: Region of protected polymorphisms with parameters s_1 and s_2

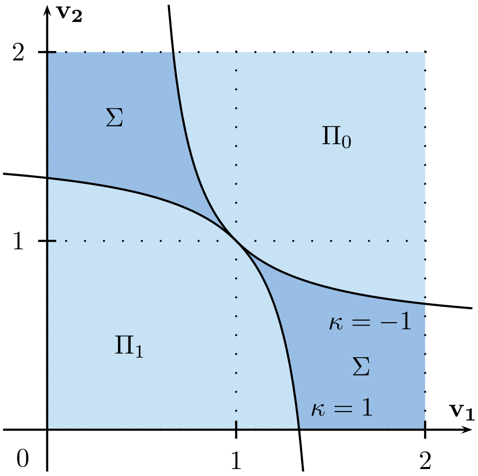

Fig. 5.11: Region of protected polymorphisms with parameters v_1 and v_2

Figure 5.10), and then the area of protected polymorphisms Σ. By (5.141) we need to calculate:

$$\begin{aligned}\Lambda &= \int_{-1}^{0}\int_{0}^{\frac{s_1}{2s_1-1}} 1\, ds_2\, ds_1 = \int_{-1}^{0} s_1 \frac{1}{2s_1-1}\, ds_1 = \\ &= \left[s_1 \frac{1}{2} \ln|2s_1-1| \right]_{-1}^{0} - \int_{-1}^{0} 1 \frac{1}{2} \ln|2s_1-1|\, ds_1 = \\ &= \frac{1}{2}\ln|-3| - \frac{1}{2}\frac{1}{2}\Big[(2s_1-1)\ln|2s_1-1| - (2s_1-1)\Big]_{-1}^{0} = \\ &= \frac{1}{2}\ln 3 - \frac{1}{4}\left[(-1)\ln|-1| + 1 + 3\ln|-3| - 3\right] = \\ &= \frac{1}{2}\ln 3 + \frac{1}{4}\ln 1 + \frac{1}{2} - \frac{1}{4} 3 \ln 3 = \\ &= \frac{2-\ln 3}{4} \\ &= 0.225347\end{aligned}$$

Thus, the area of protected polymorphisms is $\Sigma = 2 - 4 \cdot \Lambda = 1.09861$. Since the volume of the whole parameter space is $2^2 = 4$, we obtain a percentage of 27.4653%, which designates the ratio at which a protected polymorphism exists.

Numerical Analysis

In addition to our calculations, we implemented our model in Octave 3.0.2. The source code can be found in the Appendix. We begin with adapting the Levene dynamics (5.102) to the case of no dominance. Therefore, we transform the classical selection viability function for one locus, two alleles and random mating:

$$\begin{aligned} f_k(p) &= \frac{u_k p^2 + p(1-p)}{u_k p^2 + 2p(1-p) + v_k(1-p)^2} \\ &= \frac{p((1+s_k)p + 1 - p)}{(1+s_k)p^2 + 2p(1-p) + (1-s_k)(1-p)^2} \\ &= \frac{p(s_k p + 1)}{p^2 + s_k p^2 + 2p - 2p^2 +^2 p + p^2 - s_k + 2s_k p - s_k p^2} \\ &= \frac{p(s_k p + 1)}{1 - s_k + 2ps_k}. \end{aligned} \tag{5.145}$$

Now $f(p)$ depends only on s_k and, as the text below (5.102) explains, it suffices to investigate the evolution of $p = p_{1,k}$, the allelic frequency of A in niche k.

We choose s_k randomly and uniformly distributed in the interval $(-1, 1)$. Then we set an inital value for p close to 0, and another one close to 1 and calculate for each value the equilibrium it is converging to. We further assume that an equilibrium is reached if $|p - p^{'}| \leq 10^{-8}$. Then we need to check whether the respective equilibrium is internal or not. We suppose that it is internal if $p > 10^{-4}$. If this is the case for both initial frequencies, then there exists a protected polymorphism. We made 10.000 repetitions and gained the results shown in Table 5.10.

	Repetitions	Protected Polymorphism	Percentage
$s_k \in (-1, 1)$	10000	2737	27.37%

Table 5.10: Numerical result for no dominance

Hence, we see that our numerical results, which contain randomness and rounding errors, are in accordance with our analytical analysis.

Intermediate Dominance

We now assume that each heterozygote has an intermediate fitness value between the homozygotes in every niche (3.6). Our usual parametrisation of the fitness values can be seen in Table 3.1, with $u_k, v_k > 0$, $u_k, v_k \in (0, Z]$ and $Z > 1$. We have locally directed selection, thus, $u_k \leq 1 \leq v_k$ or $v_k \leq 1 \leq u_k$ in every niche. For the same reasons as in the preceding subsection, we will choose the equivalent parametrisation shown in Table 5.11 with $r_k \in [-Z, 1)$, $s_k \in (-1, Z]$, and $Z > 0$. The condition of intermediate dominance then becomes $s_k \leq 0 \leq -r_k$ or $-r_k \leq 0 \leq s_k$ in every niche, thus, $r_k s_k > 0$ for every $k \in \mathcal{K}$.

Genotypes	AA	Aa	aa
Relative Fitness Values	$1 + s_k$	1	$1 - r_k$

Table 5.11: Relative fitness values designating intermediate dominance

In order to apply Lemma 5.22, the parameters need to additionally satisfy $r_1 r_2 < 0$ and $s_1 s_2 < 0$. We define the set V by

$$V = \{w = (r_1, r_2, s_1, s_2) \in \mathbb{R}^4 : \text{A protected polymorphism exists}\}. \tag{5.146}$$

In this 4-dimensional space, we obtain 16 possibilities for the sign structure (r_1, r_2, s_1, s_2). Out of these 16 possible areas of parameter combinations, 12 are immediately excluded by the intermediate dominance assumption. The following two sets V_3 and V_4 cannot be in V since there cannot exist a protected polymorphism if an allele is the fittest in both demes which corresponds to the assumptions of Lemma 5.22.

$$\begin{aligned} V_3 &= \{w \in \mathbb{R}^4 : r_1 > 0, r_2 > 0, s_1 > 0, s_2 > 0\}, \\ V_4 &= \{w \in \mathbb{R}^4 : r_1 < 0, r_2 < 0, s_1 < 0, s_2 < 0\}. \end{aligned} \tag{5.147}$$

Thus, from all possible areas of parametric combinations, only

$$V_1 = \{w \in \mathbb{R}^4 : r_1 < 0, r_2 > 0, s_1 < 0, s_2 > 0\} \tag{5.148}$$

and

$$V_2 = \{w \in \mathbb{R}^4 : r_1 > 0, r_2 < 0, s_1 > 0, s_2 < 0\} \tag{5.149}$$

can intersect with V. In order for a protected polymorphism to exist, Lemma 5.22 tells us that the fitness values need to additionally satisfy

$$\frac{1}{r_2} + \frac{1}{r_1} < 2 \qquad \text{and} \qquad \frac{1}{s_2} + \frac{1}{s_1} > -2. \tag{5.150}$$

By distinguishing the different cases, as we demonstrated in detail in the previous subsection, we again obtain the regions, in which allele A and a are protected. Obviously, they depend on four variables.

Principle 5.27 suggests that if a protected polymorphism exists, it is a unique stable polymorphic equilibrium, provided that extreme selection patterns are excluded.

We calculate the ratio at which a protected polymorphism occurs for (i) $Z = 1$, (ii) $Z = z$ and (iii) $Z = \infty$.

(i) We choose the interval boundary $Z = 1$, thus, $r_k, s_k \in (-1, 1)$. We illustrate the area of parameter combinations in V_1 that entails a protected polymorhism, thus, $V_1 \cap V$ and denote it by Σ_1. Therefore, we plot the curves given implicitly by (5.150).

We obtain the volume of protection of both alleles, Σ_1 which is marked in Figure

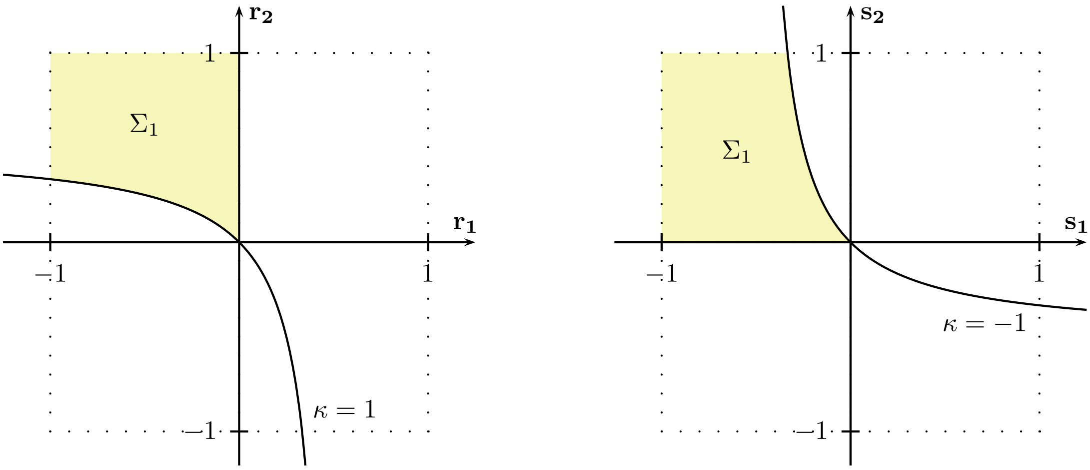

Fig. 5.12: The yellow area indicates $\Sigma_1 = V_1 \cap V$ or, rather, its intersection with the $r_1 r_2$ plane (left panel) and with the $s_1 s_2$ plane (right panel).

5.12, by calculating the measure:

$$\begin{aligned}
&\int_0^1 \int_{-1}^{\frac{s_2}{-2s_2-1}} \int_{-1}^{0} \int_{\frac{r_1}{2r_1-1}}^{1} 1 \, dr_2 \, dr_1 \, ds_1 \, ds_2 = \\
&= \int_0^1 \int_{-1}^{\frac{s_2}{-2s_2-1}} \int_{-1}^{0} 1 - \frac{r_1}{2r_1-1} \, dr_1 \, ds_1 \, ds_2 = \\
&= \int_0^1 \int_{-1}^{\frac{s_2}{-2s_2-1}} \frac{2+\ln 3}{4} \, ds_1 \, ds_2 = \\
&= \int_0^1 \frac{2+\ln 3}{4} \left(\frac{s_2}{-2s_2-1} + 1 \right) ds_2 = \\
&= \left(\frac{2+\ln 3}{4} \right)^2 = \\
&= 0.600087
\end{aligned}$$

Due to symmetry we obtain the same result for the volume of Σ_2, which equals $V_2 \cap V$, by integrating

$$\int_0^1 \int_{-1}^{\frac{s_1}{-2s_1-1}} \int_{-1}^{0} \int_{\frac{r_2}{2r_2-1}}^{1} 1 \, dr_1 \, dr_2 \, ds_2 \, ds_1 .$$

The corresponding region is marked in Figure 5.13.

Since $Z = 1$, the volume of the whole parameter space in the 4-dimensional space is $2^4 = 16$. By our assumption of intermediate dominance, the parameter space gets restricted to $V_1 \cup V_2 \cup V_3 \cup V_4$, and consequently, the volume of admissible parameters equals 4. We obtain a percentage of $2 \cdot 0.600087/4 = 30.00435\%$ where $2 \cdot 0.600087 = 1.20017$ is the volume of $\Sigma_1 \cup \Sigma_2$. Thus, we calculated the ratio at which we would expect a protected polymorphism to occur under the assumption of intermediate dominance.

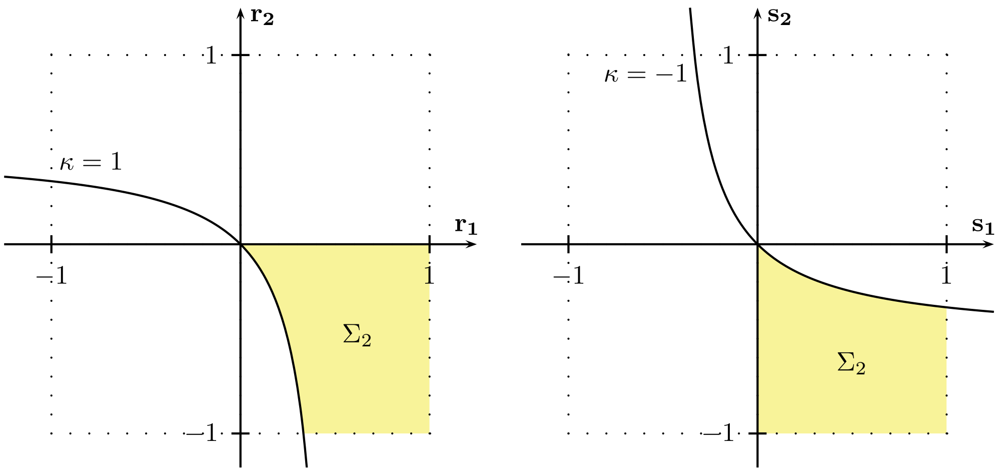

Fig. 5.13: The yellow area indicates $\Sigma_2 = V_2 \cap V$ or, rather, its intersection with the $r_1 r_2$ plane (left panel) and with the $s_1 s_2$ plane (right panel).

We know that only the parameter region $V_1 \cup V_2$ has a sign structure that enables protected polymorphisms. Therefore, we restrict attention to the region $V_1 \cup V_2$. Consequently, we obtain a percentage of $2 \cdot 0.600087/2 = 60.0087\%$ at which a protected polymorphism occurs. We want to point out that, here, we consider only $\frac{1}{2}$ of the parameter space that obeys intermediate dominance. We already established that due to symmetry, the volume of Σ_1 equals that of Σ_2 and the volume of V_1 equals that of V_2. Consequently, it suffices to calculate the volume of Σ_k and devide it by the volume of V_k for either $k = 1$ or $k = 2$ in order to obtain this ratio.

(ii) We investigate the general case, when $Z = z$, with $z > 0$ and $z \neq \infty$. We recall that the parameters r_k are now in the interval $[-z, 1)$ and s_k in $(-1, z]$, respectively. In order to obtain the volume of Σ_1, we need to calculate the following integral:

$$\begin{aligned}
&\int_0^z \int_{-1}^{\frac{s_2}{-2s_2-1}} \int_{-z}^0 \int_{\frac{r_1}{2r_1-1}}^1 1 \, dr_2 \, dr_1 \, ds_1 \, ds_2 = \\
&= \int_0^z \int_{-1}^{\frac{s_2}{-2s_2-1}} \int_{-z}^0 1 - \frac{r_1}{2r_1 - 1} \, dr_1 \, ds_1 \, ds_2 = \\
&= \int_0^z \int_{-1}^{\frac{s_2}{-2s_2-1}} \frac{2z + \ln|-1-2z|}{4} \, ds_1 \, ds_2 = \\
&= \left[\frac{2z + \ln(1+2z)}{4} \right]^2 . \qquad (5.151)
\end{aligned}$$

The volume of V_1 equals z^2, consequently, the ratio at which a protected polymorphism occurs in the parameter space $V_1 \cup V_2$ is

$$\frac{1}{4} \left[1 + \frac{\ln(1+2z)}{z} + \left(\frac{\ln(1+2z)}{2z} \right)^2 \right] . \qquad (5.152)$$

(iii) We let z go to infinity and obtain from (5.152) that

$$\begin{aligned}
&\lim_{z\longrightarrow\infty}\frac{1}{4}\left[1+\frac{\ln(1+2z)}{z}+\left(\frac{\ln(1+2z)}{2z}\right)^2\right]= \\
&=\frac{1}{4}+\lim_{z\longrightarrow\infty}\frac{\ln(1+2z)}{z}+\frac{1}{4}\left[\lim_{z\longrightarrow\infty}\frac{\ln(1+2z)}{z}\right]^2= \\
&=\frac{1}{4},
\end{aligned} \tag{5.153}$$

since $\ln(x) = o(x^{\varepsilon})$, for $\varepsilon > 0$ and $x \longrightarrow \infty$. Thus, the percentage is decreasing as z is increasing. Provided intermediate dominance and restriction to the parameter space $V_1 \cup V_2$, the ratios at which a protected polymorphism occurs converge to $\frac{1}{4}$ as $z \longrightarrow \infty$.

Numerical Results

We start by choosing r_1 randomly and uniformly distributed in the interval (-Z+1,1). Depending on whether r_1 is positve or negative, we define one of the two allowed areas of parameter combinations (5.148) or (5.149) by choosing r_2, s_1, s_2 accordingly. Then we transform the fitness values into u_1, u_2, v_1 and v_2 and insert these values in (5.102). Again, proceeded as we did for the case of no dominance, we choose two initial values for p, one close to zero and another one close to one. We iterate the Levene dynamics until $|p-p^{'}| < 10^{-8}$, in order to obtain the equilibria they are converging to. Checking whether these equilibria fulfill our internal assumption $p < 10^{-4}$, we get either an internal stable equilibrium, thus, a protected polymorphism, or not. Executing this procedure 10000 times for $w = (r_1, r_2, s_1, s_2) \in V_1 \cup V_2$ leads to the results shown in Table 5.12.

	Repetitions	Protected Polymorphism	Percentage
$Z = 1$	10000	6016	60.16%
$Z = 10$	10000	3357	33.57%
$Z = 100$	10000	2704	27.04%

Table 5.12: Numerical results for intermediate dominance with $w = (r_1, r_2, s_1, s_2) \in V_1 \cup V_2$.

5.4.2 Two Alleles and Three Demes

We assume that there is no dominance and investigate numerically for the case of two alleles and three niches, how big the volume of the parameter space is, such that a protected polymorphism is generated. Thus, providing the fitness values of Table 5.8, we choose s_1, s_2 and s_3 randomly and uniformly distributed in the interval $(-1, 1)$. The dynamics are given by 5.145. The relative niche sizes shall be equal, thus, $c_1 = c_2 = c_3 = \frac{1}{3}$. Since we have again two alleles, the simplex remains the interval $[0, 1]$. Therefore, it suffices to observe the evolution of the allelic frequency of allele A,

$p = p_1$, since $p_2 = 1 - p_1$. Again we want to point out that in the Levene model after one generation of migration the allelic frequencies are the same in every niche and, consequently, they are independent of k.

By modeling this example, we approximate the fraction at which a protected polymorphism exists relative to the total volume of the parameter space. Since we assume three niches, the parameter space is 3-dimensional, and its volume is $2^3 = 8$. Therefore, we extend the existing program from Subsection 5.4.1 by one more niche, and obtain the result given in Table 5.13. We know that a protected polymorphism cannot occur if allele A is the fittest or weakest allele in every niche. Consequently, the parameter combinations

	Repetitions	Protected Polymorphism	Percentage
$s_k \in (-1, 1)$	10000	4436	44.36%

Table 5.13: Numerical result for two alleles and three niches

$$\begin{aligned} V_8 &= \{w \in \mathbb{R}^3 : w = (s_1 < 0, s_2 < 0, s_3 < 0)\} \\ V_7 &= \{w \in \mathbb{R}^3 : w = (s_1 > 0, s_2 > 0, s_3 > 0)\} \end{aligned} \tag{5.154}$$

can be excluded, and the volume of the parameter space reduces to 6. From Subsection 5.3.2 we deduce that a protected polymorphism exists if

$$\frac{1}{s_1} + \frac{1}{s_2} + \frac{1}{s_3} < 3, \tag{5.155}$$

and

$$\frac{1}{s_1} + \frac{1}{s_2} + \frac{1}{s_3} > -3. \tag{5.156}$$

These considerations are helpful for the analytical analysis, which we do not perform here.

5.4.3 Two Alleles and Four Demes

Analogously to the previous subsection, we suppose no dominance and obtain numerically the percentage at which a protected polymorphism exists in the case of two alleles and four demes, where $c_1 = c_2 = c_3 = c_4 = \frac{1}{4}$. Providing the fitness values shown in Table 5.8, the volume of the total parameter space is $2^4 = 16$, since the dynamics (5.145) are now depending on the four variables s_1, s_2, s_3 and s_4. According to this total volume, the result is given in Table 5.14.

	Repetitions	Protected Polymorphism	Percentage
$s_k \in (-1, 1)$	10000	5647	56.47%

Table 5.14: Numerical result for two alleles and four niches

5.4.4 Three Alleles and Two Demes

We assume no dominance and obtain from Theorem 5.9 that in the case of three alleles and two demes, there can be generically at most two alleles at equilibrium. Thus, a fully polymorphic equilibrium can not exist. We numerically investigate how big the volume of the parameter space is, such that one or two alleles, respectively, will be maintained at a stable equilibrium. We will always assume that there are initially three alleles present in the population.

The dynamics of the Levene model if there is no dominance are given by (5.32) and (5.33). We choose the allelic fitnesses v_1, v_2 and v_3 randomly and uniformly distributed in $(0,1)$. We will calculate the ratios according to the total volume of the parameter space. The niche sizes shall be equal, thus, $c_1 = c_2 = \frac{1}{2}$. It suffices to investigate the change of the allelic frequencies p_1 and p_2, since $p_3 = 1 - p_1 - p_2$.

We know from our delineations above that every trajectory that starts in the interior converges to the boundary. Theorem 5.5 tells us that this equilibrium point is unique and and globally attracting. The program we implemented in Octave checks whether the trajectory from an internal initial value converges to one of the vertices, or to an equilibrium on the edge. Consequently, we obtain the ratio of fixation of one allele or the fraction at which two alleles remain in the population. Since, one of the two cases needs to occur, the two ratios need to sum to 100%. Due to randomness and rounding errors, we cannot exactly expect this from our results which are given in Table 5.15.

	Repetitions	Stable Equilibria	Percentage
One Allele	10000	7658	76.58%
Two Alleles	10000	2356	23.56%

Table 5.15: Numerical results for three alleles and two niches

5.4.5 Three Alleles and Three Demes

We assume that there is no dominance and investigate the case of three alleles and three demes. The dynamcis are again given by (5.32) and (5.33). The niche sizes shall be equal, thus, $c_1 = c_2 = c_3 = \frac{1}{3}$. We choose v_1, v_2, and v_3 randomly, and uniformly distributed in $(0,1)$. We will calculate the ratios according to the total volume of the parameter space.

First, we are interested in the percentage at which three alleles remain in the population. Again, we assume that there are always three alleles initially present. Thus, we look for the ratio at which fully polymorphic equilibria are generated. We obtain from Theorem 5.5 that if there exists an internal equilibrium, it is globally attracting. Consequently, it suffices to check whether a trajectory that starts in the interior remains in the interior.

Additionally, we investigate how big the volume of the parameter space is, such that one or two alleles, respectively, are maintained in the population. We implement this problem in Octave by testing if a trajectory that starts in the interior converges the boundary. We distinguish whether the equilibrium is one of the vertices or on an edge, to obtain the ratio of fixation of an allele and the fraction of two alleles at equilibrium. Thus, we proceed analogously to the preceeding subsection.

Since either one, two, or three alleles are maintained in the population, the three ratios need to sum to 100%. Numerically we do not expect to achieve this value. The numerical results for the ratios at which one, two, or three alleles are maintained in the population, respectively, are given in Table 5.16.

	Repetitions	Stable Equilibria	Percentage
One Allele	10000	5939	59.39%
Two Alleles	10000	3803	38.03%
Three Alleles	10000	250	2.50%

Table 5.16: Numerical results for three alleles and three niches

5.4.6 Three Alleles and Four Demes

We assume that there is no dominance and investigate analogously the case of three alleles and four niches. We extend the program from the previous subsection by one more niche. The dynamics are given by (5.32) and (5.33) and we suppose equal deme sizes, thus, $c_1 = c_2 = c_3 = c_4 = \frac{1}{4}$. The numerical ratios at which one, two, or three alleles, respectively, are maintained in the population are given in Table 5.17.

	Repetitions	Stable Equilibria	Percentage
One Allele	10000	4729	47.29%
Two Alleles	10000	4640	46.40%
Three Alleles	10000	593	5.93%

Table 5.17: Numerical results for three alleles and three niches

CHAPTER 6

SUMMARY

This work provides an overview on basic results about equilibrium and dynamical properties of selection-migration models. For the special case of the Levene model, it gives a much more detailed treatment.

The selection-migration model with weak migration can be seen as a perturbation of the pure-selection model. In particular, every locally asymptotically stable equilibrium under pure selection possesses always exactly one locally asymptotically stable equilibrium in its neighborhood with weak migration. Utilizing this result, we present some examples for multiple alleles and multiple demes, such that a fully protected polymorphism is generated under weak migration.

In the case of two alleles and two niches, an unstable boundary equilibrium of the pure-selection migration model can move out of the simplex if a weak migraton flow is introduced.

For two alleles, arbitrarily many niches and underdominance in every niche, we observed that the number of locally stable equilibria is 2^K provided there is weak migration. This exponential increase of equilibria stands in contrast to the linear increase of equilibria in the Levene model, where we determined the maximum number of stable equilibria to be $K + 1$.

The emphasis of this work is laid on the Levene model, which is a special case of a selection-migration model. In the Levene model, we have convergence of all trajectories to some equilibrium (point or manifold). Further, in the case of soft selection, the geometric mean fitness w^* is a Lyapunov function. If there exists a proteced polymorphism in the Levene model with two alleles, then all trajectories converge to some stable internal equilbrium point (no manifold).

For a population with two alleles, we addressed the issue of how big the volume of the parameter space is, such that a protected polymorphism exists.

- In the case of no dominance and two niches, the percentage at which a protected polymorphism occurs is 27.47% with respect to the whole parameter space. We increased the number of demes to three and four niches and obtained numerically a ratio of 44.36% and 56.47%, respectively.

- In the case of intermediate dominance and two demes, we observed that the ratio at which a protected polymorphism occurs is decreasing as the interval of admissible parameters increases. Thus, by calculating the limit, we found that this ratio converges to $\frac{1}{4}$ with respect to the restricted parameter space which has a sign structure that enables protected polymorphisms. We derived this result analytically and obtained according results by numerical simulations.

Further, we considered a population with three alleles and calculated numerically the ratios at which one, two, or three alleles, respectively, are maintained in the population provided no dominance.

- We started our investigations with two demes for which a fully polymorphic equilibrium can not exist. We obtained a ratio of 23.56% for two alleles being at equilibrium, and a percentage of 76.78% for fixation of one allele.
- For three demes, the numerical percentage that all three alleles are maintained in the population is 2.5%, the ratio that two alleles are at equilibrium is 38.03%, and fixation of one allele occurs at a frequency of 59.39%.
- Supposing four demes, we obtained for three, two, and one alleles being at equilibrium the ratios 5.93%, 46.40%, and 47.27%, respectively.

Thus, provided three alleles and no dominance, we could observe that with an increase in the number of niches, the ratios of equilibria at which two, or three alleles occur grow, whereas the percentage of fixation states declines. Both the frequencies of stable equilibria with two and with three alleles increase with the number of demes, whereas the frequency of stable monomorphic equilibria decreases correspondingly.

APPENDIX

PSTricks Source Codes

We only present the source codes of Figure 5.2 and 5.10. The other graphics were generated in a similar way.

Listing 1: fig5-2.tex

```
\documentclass{article}
\usepackage{pst-plot, pstricks}
\usepackage{fancybox,amssymb,color}
\pagestyle{empty}
\parindent=0pt
\newpsobject{showgrid}{psgrid}{subgriddiv=1,griddots=10,gridlabels=0pt}

\begin{document}
\psset{unit=5cm}
   \begin{pspicture}(-0.125,-0.125)(1.125,1.125)
   \showgrid
   \psaxes{->}(0,0)(-0.125,-0.125)(1.125,1.125)

   \psplot[plotstyle=curve]{0}{1}{x}
   \psplot[plotstyle=curve,linecolor=red]{0}{1}{3.34512 x x mul mul 0.5 x mul
       add 0.5 x x mul mul sub 6.69024 x x mul mul 2 x mul add 2 x x mul mul
       sub 0.11626 add 0.23252 x mul sub 0.11626 x x mul mul add div 0.06598 x
       x mul mul 0.5 x mul add 0.5 x x mul mul sub 0.13196 x x mul mul 2 x mul
       add 2 x x mul mul sub 2.98791 add 5.97582 x mul sub 2.98791 x x mul mul
       add div add}
   \psline[dotsize=7pt]{o-}(0,-0.22)(0.39,-0.22)
   \psline[dotsize=7pt, arrowsize=7pt]{>-*}(0.35368,-0.22)(0.59684,-0.22)
   \psline[dotsize=7pt, arrowsize=7pt]{-<}(0.59684,-0.22)(0.84,-0.22)
   \psline[dotsize=7pt]{-o}(0.81,-0.22)(1,-0.22)
   \psline[linestyle=dashed](0.59684,-0.125)(0.59684,0.59484)

   \rput(1.08,0.06){$p$}
   \rput(0.07,1.1){$p^{'}$}
   \rput(-0.075,-0.075){$0$}
   \end{pspicture}
\end{document}
```

Listing 2: fig5-9.tex

```
\documentclass{article}
\usepackage{pst-plot, pstricks}
```

```
\usepackage[usenames]{pstcol}
\usepackage{fancybox,amssymb,color}
\pagestyle{empty}
\parindent=0pt
\newpsobject{showgrid}{psgrid}{subgriddiv=1,griddots=10,gridlabels=0pt}

\begin{document}
\psset{unit=2.5cm}
\definecolor{mylightblue}{cmyk}{0.20,0.04,0,0}
\definecolor{myblue}{cmyk}{0.38,0.15,0,0}
   \begin{pspicture}(-1.25,-1.25)(1.25,1.25)
   \psframe*[linecolor=mylightblue](-1,-1)(1,1)

      \begin{psclip}{\psframe[linestyle=none](-1,0)(0,1)}
      \psset{hatchsep=11pt, fillstyle=hlines}
         \pscustom[linestyle=none]{
         \psplot[plotstyle=curve]{-1}{0}{x 2 x mul 1 sub div}
         \lineto(-1,0)
         }
      \end{psclip}

   \showgrid
   \psaxes{->}(0,0)(-1.25,-1.25)(1.25,1.25)

      \begin{psclip}{
      \pscustom[linestyle=none]{
         \psplot[plotstyle=curve]{-1}{0.333333333}{x 2 x mul 1 sub div}
         \lineto(1,-1)
         \lineto(1,1)
         \lineto(-1,1)
         }
      \pscustom[linestyle=none]{
         \psplot[plotstyle=curve]{-0.357142857}{1.25}{x 0 2 sub x mul 1 sub div}
         \lineto(1,-1)
         \lineto(-1,-1)
         \lineto(-1,1)
         }
      }
      \psframe*[linecolor=myblue](-1,-1)(1,1)
      \end{psclip}

   \psplot[plotstyle=curve]{-1.25}{0.357142857}{x 2 x mul 1 sub div}
   \psplot[plotstyle=curve]{-0.357142857}{1.25}{x 0 2 sub x mul 1 sub div}

   \rput(1.2,0.09){$\mathbf{s_1}$}
   \rput(0.12,1.2){$\mathbf{s_2}$}
   \rput(0.56,-0.88){$\kappa=1$}
   \rput(0.71,-0.43){$\kappa=-1$}
   \rput(0.535,0.55){$\Pi_1$}
   \rput(-0.55,-0.55){$\Pi_0$}
   \rput(0.66,-0.665){$\Sigma$}
   \rput(-0.645,0.655){$\Sigma$}
   \rput(-0.79,0.14){\colorbox{myblue}{$\Lambda$}}
   \end{pspicture}
\end{document}
```

Octave Source Codes

We implemented the calculations needed for simulating the evolution of the allelic frequencies in our models in Octave 3.0.2. Find enclosed some of the corresponding .m-files.

The following .m-file was used to execute the necessary repetitions of our models.

Listing 3: repeat.m

```
function result = repeat
   sum = 0;
for i = 1:10000
   tmp = polyornotnodom;
   if tmp == 1
      sum = sum+1;
   end
end
result = sum;

endfunction
```

The following two codes were used for the Levene model with two alleles and two niches, provided no dominance.

Listing 4: polyornotnodom.m

```
function value = polyornotnodom

% Fitness values s1 and s2 are generated in (-1,1).
s1 = rand*2-1;
s2 = rand*2-1;

% Setting an inital value for p close to zero and another one close to one.
p0 = 0.0001;
p1 = 0.9999;

% Starting from p0 or p1, equilibria equ0 and equ1 are getting reached.
equ0 = iteratenodom(p0,s1,s2);
equ1 = iteratenodom(p1,s1,s2);

% An equilibrium is said to be internal if p > 10^(-4).
if equ0 > 0.0001 & equ1 < 0.9999
   value = 1;
else
   value = 0;
end

endfunction
```

Listing 5: iteratenodom.m

```
function equ = iteratenodom (p,s1,s2)

% Suppose equal deme sizes.
c1 = 0.5;
c2 = 0.5;

% Selection function for no dominance.
fknodom = @(sk,pk)(pk*(1+sk*pk))/(1-sk+2*pk*sk);

% Calculating one round of selection and migration in the Levene model.
pprime = c1*fknodom(s1,p)+c2*fknodom(s2,p);

% An equilibrium shall be reached if |p-pprime| <= 10^(-8).
while abs(p-pprime)>0.00000001
   pprimeprime = c1*fknodom(s1,pprime)+c2*fknodom(s2,pprime);
   p = pprime;
   pprime = pprimeprime;
end

```

```
equ = pprime;

endfunction
```

The following two codes were used for the Levene model with two alleles and two niches, provided intermediate dominance.

Listing 6: polyornotintdom.m

```
function value = polyornotintdom

% We choose the boundary of the intervals (-Z+1,1) and (-1,Z-1).
Z=10;

% We choose r1 randomly in (-Z+1,1).
r1=-rand*(Z+1)+1;

% Depending on r1, we obtain r1<0, r2>0, s1<0, s2>0 or r1>0, r2<0, s1>0, s2<0.
if r1 > 0
   r2 = -rand*Z;
   s1 = rand*Z;
   s2 = -rand;
elseif r1 < 0
   r2 = rand;
   s1 = -rand;
   s2 = rand*Z;
else
% The case r1=1/2 shall be marked and consequently, be excluded.
   value = 10000;
   break;
end

% We calculate n1=[u1 v1] and n2=[u2 v2].
n1 = [1+s1 1-r1];
n2 = [1+s2 1-r2];

% We set the initial values.
p0 = 0.0001;
p1 = 0.9999;

% We calculate the equilibria reached from the starting points p0 and p1.
glg0 = iterateintdom(p0,n1,n2);
glg1 = iterateintdom(p1,n1,n2);

% An equilibrium shall be internal if p > 10^(-4).
if glg0>0.0001 & glg1<0.9999
   value = 1;
else
   value = 0;
end

endfunction
```

Listing 7: iterateintdom.m

```
function equ = iterateintdom (p,n1,n2)

% Suppose equal deme sizes.
c1=0.5;
c2=0.5;

% Viability selection function for two alleles, one locus and random mating.
fk=@(uk,vk,pk)(uk*pk*pk+pk*(1-pk))/(uk*pk*pk+2*pk*(1-pk)+vk*(1-pk)*(1-pk));

% We calculate one round of selection and migration.
```

```
pprime=c1*fk(n1(1),n1(2),p)+c2*fk(n2(1),n2(2),p);

% An equilibrium shall be reached, when |pstrich - p| <= 10^(-8).
while abs(p-pprime)>0.00000001
   pprimeprime=c1*fk(n1(1),n1(2),pprime)+c2*fk(n2(1),n2(2),pprime);
   p=pprime;
   pprime=pprimeprime;
end

equ=pprime;

endfunction
```

The following four codes were used for the Levene model with three alleles and three niches, provided no dominance. They determine if one, two, or three alleles are at equilibrium, respectively. The last code executes the iterations of the Levene model.

Listing 8: polyornotnodom33one.m

```
function value = polyornotnodom33one

% The fitness values v_k=[v_{1,k} v_{2,k} v_{3,k}] are chosen randomly.
v1=[rand rand rand];
v2=[rand rand rand];
v3=[rand rand rand];

% Initial value for the allelic frequency p.
pint = [0.4;0.3];

% The equilibrium that will be reached starting from pint.
equpint = iteratenodom6(pint,v1,v2,v3);

% The equilibrium is a fixation state if p>1-10^(-4) for any component.
if equpint(1)>0.9999 | equpint(2)>0.9999 | (1-equpint(1)-equpint(2))>0.9999
        value = 1;
else
        value = 0;
end

endfunction
```

Listing 9: polyornotnodom33two.m

```
function value = polyornotnodom33two

% The fitness values v_k=[v_{1,k} v_{2,k} v_{3,k}] are chosen randomly.
v1=[rand rand rand];
v2=[rand rand rand];
v3=[rand rand rand];

% Initial value for the allelic frequency p.
pint = [0.4;0.3];

% The equilibrium that will be reached starting from pint.
equpint = iteratenodom6(pint,v1,v2,v3);

% Two alleles are at equilibrium if exactly one component of p is <10^(-4).
if (equpint(1)<0.0001 & equpint(2)>0.0001 & (1-equpint(1)-equpint(2))>0.0001) |
    (equpint(1)>0.0001 & equpint(2)<0.0001 & (1-equpint(1)-equpint(2))>0.0001)
    | (equpint(1)>0.0001 & equpint(2)>0.0001 & (1-equpint(1)-equpint(2))<0.0001)
   value = 1;
else
   value = 0;
end
```

```

endfunction
```

Listing 10: polyornotnodom33three.m

```
function value = polyornotnodom33three

% The fitness values v_k=[v_{1,k} v_{2,k} v_{3,k}] are chosen randomly.
v1=[rand rand rand];
v2=[rand rand rand];
v3=[rand rand rand];

% Initial value for the allelic frequency p.
pint = [0.4;0.3];

% The equilibrium that will be reached starting from pint.
equpint = iteratenodom33(pint,v1,v2,v3);

% The equilibrium is internal if p > 10^(-4) for every component.
if equpint(1)>0.0001 & equpint(2)>0.0001 & (1-equpint(1)-equpint(2))>0.0001
   value = 1;
else
   value = 0;
end

endfunction
```

Listing 11: iteratenodom33.m

```
function equ = iteratenodom33 (p,v1,v2,v3)

% Suppose equal deme sizes.
c1 = 1/3;
c2 = 1/3;
c3 = 1/3;

% Selection function when there is no dominance and three alleles.
fknodom = @(vk,pk)([vk(1)/(vk(1)*pk(1)+vk(2)*pk(2)+vk(3)*(1-pk(1)-pk(2)));
    vk(2)/(vk(1)*pk(1)+vk(2)*pk(2)+vk(3)*(1-pk(1)-pk(2)))]);

% Calculating one round of selection and migration in the Levene model.
pprime = 0.5.*p.*(c1.*fknodom(v1,p)+c2.*fknodom(v2,p)+c3.*fknodom(v3,p)+1);

% An equilibrium shall be reached if |p-pprime| <= 10^(-8) for every component.
while any(abs(p-pprime)>0.00000001)
   pprimeprime = 0.5.*pprime.*(c1.*fknodom(v1,pprime)+c2.*fknodom(v2,pprime)
       +c3.*fknodom(v3,pprime)+1);
   p = pprime;
   pprime = pprimeprime;
end

equ = pprime;

endfunction
```

REFERENCES

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ZUSAMMENFASSUNG

In dieser Arbeit werden die Dynamiken und einige wichtige Resultate des allgemeinen Selektions-Migrationsmodells unter besonderer Berücksichtigung des Levene Modells behandelt.

Zunächst werden allgemeine Ergebnisse bezüglich geschützter Polymorhpismen im Fall zweier Allele, Gleichgewichte wenn keine Dominanz verliegt, Fixierung eines Allels, schwacher und starker Migration sowie gleichmäßiger Selektion betrachtet.

Das Hauptaugenmerk dieser Arbeit liegt auf dem Levene Modell, für das viele Resultate gezeigt werden können, die im allgemeinen Selektions-Migrationsmodell, aufgrund der komplexeren Dynamik, nicht gelten. Im Levene Modell konvergiert jede Trajektorie zu einem Gleichgewicht (Punkt oder Mannigfaltigkeit). Weiters ist das geometische Mittel der mittleren Fitnesswerte w^* eine Lyapunovfunktion, wenn wir weiche Selektion voraussetzen. Existiert im Levene Modell mit zwei Allelen ein geschützter Polymorphismus, so konvergiert jede Trajektorie zu einem stabilen, inneren Gleichgewichtspunkt (keine Mannigfaltigkeit).

Wir gehen der Frage nach, wie groß der Parameterraum im Levene Model für zwei Allele ist, sodass ein geschützter Polymorphismus existiert. Setzen wir keine Dominanz und zwei Nischen voraus, so tritt ein geschützter Polymorphismus in 27.47% der Fälle bezüglich des gesamten, zulässigen Parameterbereiches auf. Betrachten wir das Problem numerisch im Fall von drei Nischen erhalten wir eine Rate von 44.36%, im Fall von vier Nischen beträgt diese 56.47%. Nimmt man intermediäre Dominanz und zwei Nischen an, so haben wir beobachtet, dass die Rate mit der ein geschützter Polymorphismus auftritt, mit zunehmender Intervallgröße der Fitnessparameter, abnimmt. Durch Grenzübergang konnten wir analytisch zeigen, dass diese Rate bezüglich des eingeschränkten Parameterraumes, dessen Anordnung der Vorzeichen einen geschützten Polymorphismus zulassen, gegen $\frac{1}{4}$ konvergiert. Die durch numerische Simulation erhaltenen Werte entsprechen diesen Ergebnissen.

Weiters haben wir das Levene Modell mit drei Allelen und keiner Dominanz numerisch betrachtet. Wir untersuchten mit welchem Prozentsatz ein, zwei oder drei Allele in der Population erhalten bleiben. Dadurch konnten wir beobachten, dass die Prozentsätze der polymorphen Gleichgewichte mit steigender Nischenanzahl zunehmen, und die Rate der fixierenden Gleichgewichte um genau diesen Anteil fällt.

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