# Strategy dynamics

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# ADAPTIVE DYNAMICS FOR LOTKA-VOLTERRA COMMUNITY DYNAMICS

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## ABSTRACT

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

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

## 5.1 INTRODUCTION

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

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

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

After invasion, the residents and mutants eventually home in on a (possibly unique) $c$-attractor in the community state space spanned by their population densities, or on a $c$-attractor in the community state space spanned by a subset of these densities. (Note that this addition with respect to a subset is necessary, since a $c$-attractor is assumed to lie in the interior of a community state space.) On this $c$-attractor the phenotypic composition of the community in general will be different from the one which became invaded. In case the mutant population replaces its progenitor population, we say that a *trait substitution* takes place (on the evolutionary timescale). A trait substitution leaves the number of populations that constitute the community unaltered, and corresponds to a small change in the phenotypic trait composition of the community. The direction and size of this change are determined by the specific mutant population which by chance occurs and invades the resident $c$-attractor. The probability distribution for the mutant trait values that actually do invade is determined by the possible supply of mutants and by the probability that a given mutant population actually invades. This latter probability (which we assume to be a continuous function with respect to the mutants' trait value) is up to first order determined by the so-called *local fitness gradient* at the resident attractor as determined by the trait value of the population from which the mutants emerged. It thus follows that on a given $c$-attractor there exist as many local fitness gradients as there are resident populations present on that $c$-attractor.

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

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

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

## 5.2 AN INTRODUCTION TO THE MATHEMATICAL FRAMEWORK

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

   with $\circ$ denoting the Hadamard product.

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

3. The function $a$ is assumed to be such that for each function $r$ and each choice of trait values $\tau_1,\ldots,\tau_k$, $k \geq 1$, the solutions of the Lotka-Volterra equations (5.1) are uniformly bounded for $t \to +\infty$. (The matrix $A(\tau_1,\ldots,\tau_k)$ then is called a $B$-matrix, see [49], and the uniformity holds with respect to initial conditions in $\mathbb{R}^k_+$). Thus, given $a$ and $r$, for each choice $(\tau_1,\ldots,\tau_k) \in \mathbb{T}^k$ there exists a (finite) $b(r,a,\tau_1,\ldots,\tau_k)$ such that for all $x \in \mathbb{R}^k_+$ and all $i \in \{1,\ldots,k\}$: $\limsup_{t\to+\infty} x_i(t) \leq b(r,a,\tau_1,\ldots,\tau_k)$.

4. The community state spaces $\mathbb{R}^k_+$ are provided with the sum norm, denoted by $||.||$, and the metric, denoted by $d$, and topology induced by it. (Thus, for $x = (x_1,\ldots,x_k) \in \mathbb{R}^k_+$, $||x|| = \sum_{i=1}^{k} |x_i|$, with in general $|x|$ denoting the absolute value of the real number $x$.) The sets $\mathbb{T}^k$ as well as any of their

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

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

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

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

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

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

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

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

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

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

1. $\Sigma_k$ denotes the set of permutations on $k$ elements, and $\sigma_0$ denotes the identity permutation in any $\Sigma_k$.

2. $V_{k,\sigma_0}$ denotes the subset $\{(\tau_1, \dots, \tau_k) \in \mathbb{T}^k | \tau_1 < \dots < \tau_k\}$ of $\mathbb{T}^k$. For $\sigma \in \Sigma_k$, $V_{k,\sigma}$ denotes the set $\{(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}) \in \mathbb{T}^k | (\tau_1, \dots, \tau_k) \in V_{k,\sigma_0}\}$.

3. Let $(\tau_1, \dots, \tau_k) \in \mathbb{T}^k$, and for $l \in \{1, \dots, k\}$ let $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ with $i_1 < i_2 < \dots < i_l$. Then $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$ denotes the element $(\tau_1, \dots, \tau_{i_1-1}, \tau_{i_1+1}, \dots, \tau_{i_l-1}, \tau_{i_l+1}, \dots, \tau_k) \in \mathbb{T}^{k-l}$. In case the numbers $i_1, \dots, i_l$ are not in increasing order, $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l})$ denotes the

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

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

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

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

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

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

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

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

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

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

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

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

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

**Definition 1.**

1. Two elements $(\tau_1, \ldots, \tau_k) \in \mathbb{T}^k$ and $(\tau'_1, \ldots, \tau'_{k'}) \in \mathbb{T}^{k'}$ are phenotypically equivalent if there exists a composition of a permutation of indices and/or merging or splitting that maps either one of the trait combination onto the other one.

2. Two sets $V \subset \mathbb{T}^k$ and $V' \subset \mathbb{T}^{k'}$ are said to be phenotypically equivalent if each element of $V$ is phenotypically equivalent to an element of $V'$ and vice versa.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

**Notation 4.**

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

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

2. A general rest point of $LV_k(\tau_1, \dots, \tau_k)$ in the community state space $\mathbb{R}_+^k$ will be denoted by $x^* = \left(x_1^*, \dots, x_k^*\right)$ (or, if convenient, by $\left(x_1^*, \dots, x_k^*\right)(\tau_1, \dots, \tau_k)$ or $\left(x_1^*(\tau_1, \dots, \tau_k), \dots, x_k^*(\tau_1, \dots, \tau_k)\right)$).

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

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

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

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

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

**Lemma 1.**

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

The previous Lemma implies that $a(\tau_i,\tau_i) < 0, i = 1,\ldots,k,$ is a necessary condition on the contypic interaction coefficients for the solutions of the equations (5.1) to be uniformly bounded (for any function $r$). We therefore shall assume this condition to hold from now on:

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

Continuity of the function $a$ implies:

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

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

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

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

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

and in addition

2. $\limsup\limits_{t \to +\infty} x_i(t) \leq D$ for all $i$.

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

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

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

In this paper we are i.a. interested in the fate of resident and mutant populations after emergence of the mutants from the community of residents. Due to the initially very low density of a mutant population, invasion of the environment it encounters, by increase of its density, is subject to demographic stochasticity. Whether or not a mutant population has a positive probability to invade an environment depends, amongst others, on the phenotypic trait of the mutants, and is captured by the invasion fitness of the mutants' phenotypic trait value in that environment.

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

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

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

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

Assumption 3 forms the basis for the working hypothesis that only a single successful mutant population may emerge, from a community that resides on an attractor. In the case of successful mutants we shall concentrate on those invasion attempts where the mutants make it to such densities that the deterministic description in terms of ODE's is applicable. We shall soon provide more details about the notion of attractor that we adopt in the paper.

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

**Assumption 4.**

1. We assume that when a mutant population emerges, the resident community moves along an orbit in an ep-chain attractor, which is a closed and bounded subset in the interior of the resident community dynamics state space. We shall denote such an attractor as c-attractor, where the c stems from community.

2. Throughout the paper we assume that on a c-attractor only one mutant population emerges at a time, in a very small positive density, from one of the populations present on that attractor. $M(\tau)$ denotes the set of possible phenotypic trait values of mutant populations that can emerge from the resident population with trait value $\tau$, and is called the mutational range of $\tau$. We suppose that there exist two positive numbers $\epsilon_-(\tau)$ and $\epsilon_+(\tau)$ such that $M(\tau)$ can be written as $M(\tau) = \{\nu \in \mathbb{T} | \tau - \epsilon_-(\tau) < \nu < \tau + \epsilon_+(\tau)\}$. (Note that this allows for the degenerate case in which the mutants' phenotypic trait value is equal to that of its progenitors. Mutants and progenitors then are indistinguishable, and the system of only residents is phenotypically equivalent to that of residents and mutants.) Two sets $M(\tau_i)$ and $M(\tau_j)$ are not necessarily disjoint. With $x_\nu$ we denote the mutant population's density for mutants with phenotypic trait value $\nu$.

3. After the emergence of a mutant population with trait value $\nu \in \mathbb{T}$ from a $c$-attractor for $LV_k(\tau_1, \ldots, \tau_k)$, the densities of residents and mutants develop in time according to the community-differential equations (5.1) for $LV_{k+1}(\tau_1, ..., \tau_k, \nu)$.

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

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

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

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

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

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

The parameters $\tau_1, \ldots, \tau_k$ appear in the argument of the invasion fitness function, and are separated from the mutants' trait value by means of a semicolon. By doing so we can make a clear distinction between the resident trait values and possible operations performed on them (such as a permutation, or a reduction due to absence of a resident population), and the mutants' trait value. Furthermore, by letting the parametric resident traits appear in the argument of the invasion fitness function rather than as an index to it, we adapt already here to a notation that will only become effective in the second part of the text, where we will consider functional dependence of the mutants' fitness on the resident trait values. By adopting this notation we already anticipate on the result that the invasion fitness of a phenotype is independent of the specific $c$-attractor in $\mathrm{int}(\mathbb{R}^k_+)$, or specific orbit herein, on which the mutants appear; see Corollary 3. Therefore it suffices to refer to the resident community solely by means of the phenotypic trait values present in it.

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

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

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

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

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

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

The proof of this statement goes as follows. Consider $k+1$ populations, with trait values $\tau_1,\dots,\tau_k,\tau_{k+1}$, respectively, of which the $k+1$-th population is the mutant population, with trait value $\tau_{k+1} = \tau_i$ for some $i \in \{1, \dots, k\}$, that appears on a c-attractor component for $LV_k(\tau_1, \dots, \tau_k)$. Then

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

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

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

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

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

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

(by Lemma 2), which proves the statement.

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

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

that imply the following

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

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

**Remark 3.** Corollary 2 is put slightly stronger than Theorem 5.2.3 in [49]. This Theorem assumes that the densities $x_1, \dots, x_k$ of $k$ populations develop according to a Lotka-Volterra community dynamics for which there exist a unique equilibrium density $\hat{x} = (\hat{x}_1, \ldots, \hat{x}_k) \in \mathrm{int}(\mathbb{R}^k_+)$. Then, if there exist two positive numbers $a$ and $A$ such that $a < x_i(t) < A$ for all $i$ and all $t > 0$, the average density $\overline{x}_i$ exists and equals $\hat{x}_i$.

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

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

**Notation 6.**

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

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

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

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

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

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

2. The function $s_k(\tau_1, \ldots, \tau_k; .) : \mathbb{T} \to \mathbb{R}$ inherits the differentiability properties from the functions $r$ and $a$.

3. For each $\sigma \in \Sigma_k$, and for all $\nu \in \mathbb{T}$: $s_k(\tau_1, \ldots, \tau_k; \nu) = s_k(\tau_{\sigma(1)}, \ldots, \tau_{\sigma(k)}; \nu)$.

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

**Definition 4.**

1. $\hat{x}(\lambda) = 0$.

2. $|A(\lambda)| = 1$.

3. The invasion fitness function on $\lambda$ is $s_0(\lambda; .) : \mathbb{T} \to \mathbb{R}$, $s_0(\lambda; \nu) = r(\nu)$; it will simply be denoted by $s_0$ (omitting the $\lambda$).

**Remark 4.**

1. The third statement in Corollary 4 states that the ordering of the traits present on a resident $c$-attractor does not influence the fitness of the mutants' trait. In particular this implies that the order in evolutionary time in which the resident populations were subsequently incorporated to form a $c$-attractor, does not affect the fitness of mutants that emerge from that attractor.

2. Note that the notational conventions introduced so far for elements $(\tau_1, \ldots, \tau_k)$ of $\mathbb{T}^k$ do not automatically extend to the bracket notation $\langle \tau_1, \ldots, \tau_k \rangle \in R_{int}(\mathbb{T}^k)$. E.g., the notation $\langle \tau_1, \ldots, \tau_k \setminus \tau_k \rangle$ and its identification with $\langle \tau_1, \ldots, \tau_{k-1} \rangle$ only make sense if there exists a $c$-attractor in the interior of the community state space of $LV_{k-1}(\tau_1, \ldots, \tau_{k-1})$. However, for each $\sigma \in \Sigma_k$, $\langle \tau_1, \ldots, \tau_k \rangle$ can be identified with $\langle \tau_{\sigma(1)}, \ldots, \tau_{\sigma(k)} \rangle$.

3. Two Lotka-Volterra models $LV_k(\tau_1, \ldots, \tau_k)$ and $LV_l(\tau'_1, \ldots, \tau'_l)$ that are phenotypically equivalent do not necessarily have equal collections of $c$-attractors. As a consequence the equality of functions $s_k(\tau_1, \ldots, \tau_k; .) = s_l(\tau'_1, \ldots, \tau'_l; .)$ may not hold true. In fact, let $k > l$, and suppose that $LV_k(\tau_1, \ldots, \tau_k)$ is phenotypically equivalent to $LV_l(\tau'_1, \ldots, \tau'_l)$,

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

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

**Example 1.**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

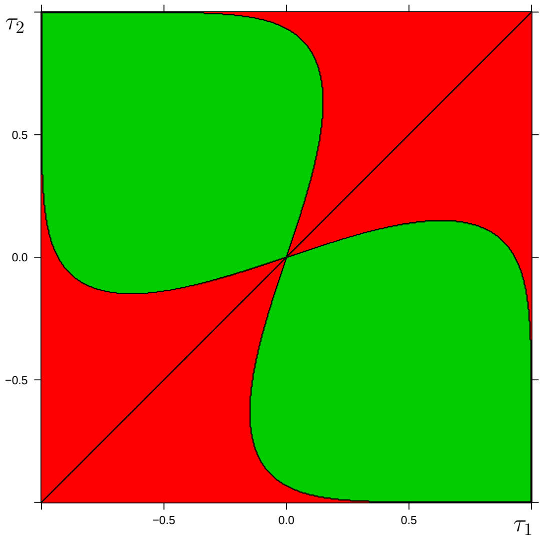

Figure 5.1: For $\mathbb{T} = [-1,1]$ and functions $r(\tau) = 1 - \tau^2$, $a(\tau_1, \tau_2) = -\dfrac{e^{-3(\tau_1-\tau_2)^2}}{1-0.5\tau_1^2}$, the main diagonal in $\mathbb{T}^2$ contains the embedded set of monomorphisms $\mathbb{A}_1 = (-1,1)$. The green region (in $(-1,1)^2$) shows the set $\mathbb{A}_2$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

and that expression (5.15) is equal to

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

The last expression can be rewritten as

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

**Remark 5.**

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

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

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

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

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

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

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

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

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

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

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

After invasion of a $c$-attractor $\langle \tau_1, \ldots, \tau_k \rangle$ by a mutant population with trait value $v = \tau_{k+1}$, the residents and mutants home in on a (possibly unique) $c$-attractor for $LV_{k+1}(\tau_1, \ldots, \tau_k, \tau_{k+1})$, or on a $c$-attractor for a $LV_l(\tau_{i_1}, \ldots, \tau_{i_l})$, with $\{i_1, \ldots, i_l\} \subset \{1, \ldots, k+1\}$. This outcome generically will depend on the trait values of the resident populations as well as that of the mutant population. Unless $LV_{k+1}(\tau_1, \ldots, \tau_k, \tau_{k+1})$ has a unique $c$-attractor to which the dynamics after invasion converges, the outcome furthermore depends on the orbit that the residents and mutants follow. This orbit in turn may depend on the specific $c$-attractor that became invaded, and on the point on that $c$-attractor where the mutants emerged. Outcomes after invasion will be discussed further in section 5.3, but a first straightforward result can already be mentioned here. Suppose a mutant population with trait value $\nu$ emerges from a $c$-attractor $\langle \tau_1, \ldots, \tau_k \rangle$. If $LV_{k+1}(\tau_1, \ldots, \tau_k, \nu)$ is permanent, then necessarily the community of residents and mutants eventually will reach a $c$-attractor $\langle \tau_1, \ldots, \tau_k, \nu \rangle$. We shall introduce the following notation for the family of permanent Lotka-Volterra models:

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

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

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

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

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

#### *Graphical devices: PIP, MIP and TEP*

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

$$s_1(\tau;\nu) = (\nu - \tau)z_1(\tau;\nu), \tag{5.21}$$

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

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

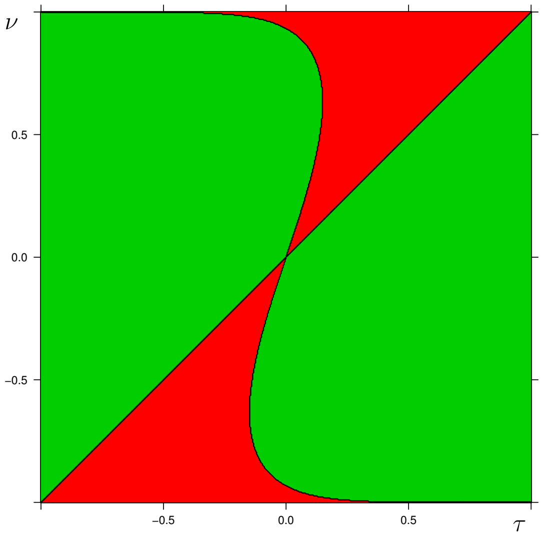

Figure 5.2: PIP for the function $s_1(\tau;\nu) = 1 - \nu^2 - \frac{e^{-3(\tau-\nu)^2}}{1-0.5\nu^2}(1-0.5\tau^2)(1-\tau^2)$ on $[-1,1]^2$. (I.e., the function $s_1$ is derived from the functions $r$ and $a$ as given in Example 1.2). The green region represents positive values, the main diagonal and the black curve represent the zero set of $s_1$, and the red region the negative values.

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

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

**Remark 6.**

1. By representing $\mathbb{A}_1$ by its embedding in the main diagonal in $\mathbb{A}_1 \times \mathbb{A}_1$, a monomorphic community dynamics parametrised by $\tau$ is split into a phenotypically equivalent dimorphic dynamics parametrised by $(\tau, \tau)$. Although $(\tau, \nu)$ (with $\nu$ a mutant of $\tau$) lies close (in a metric sense) to $(\tau, \tau)$, the dynamical behaviour of a community parametrised by $(\tau, \nu)$ generically differs from that of a community parametrised by $(\tau, \tau)$: the $(\tau, \nu)$-community generically shows competitive exclusion, whereas the $(\tau, \tau)$-community exhibits neutral coexistence. The embedding of $\mathbb{A}_k$ into $\triangle^{k+1}_{i,k+1}$, $i = 1, \ldots, k$ is taken for granted in all studies of adaptive dynamics.

2. To avoid densities from becoming infinite (which is a required constraint in any biologically inspired model involving population densities) it follows from (5.16) that within the region of mutually invadable points no points $(\tau, \nu)$ are allowed to occur in which the determinant of the interaction matrix $|A(\tau, \nu)|$ becomes 0. I.e. (by (5.19)), in $\mathbb{A}_2$ the interaction matrix determinant must be strictly positive.

3. We shall use the following color codes in PIP, MIP and TEP. In a PIP a point $(\tau_1, \tau_2)$ is coloured red if $s_1(\tau_1; \tau_2) < 0$; it is coloured green in case $s_1(\tau_1; \tau_2) > 0$, and black if $s_1(\tau_1; \tau_2) = 0$. In a MIP or TEP, a point $(\tau_1; \tau_2)$ is coloured red if either $s_1(\tau_1; \tau_2) < 0$ or $s_1(\tau_2; \tau_1) < 0$; it is coloured green if it belongs to $\mathbb{A}_2$, and black if either $s_1(\tau_1; \tau_2) = 0$ or $s_1(\tau_2; \tau_1) = 0$. In addition in $\mathbb{A}_2$ the 1- and 2-isocline (see below) will be represented by a solid and dotted black curve, respectively.

Before we continue with an analysis of the monomorphic and dimorphic adaptive dynamics, we shall first provide an example of a TEP and explain how to read this figure. Figure 5.3 shows the TEP for the function $s_1$ (i.e., the function that also underlies Figures 5.1 and 5.2). The whole main diagonal corresponds to $\mathbb{A}_1$, and the green region represents $\mathbb{A}_2$. The main diagonal is divided in two sections by the intersection of the zero set of the function $z_1$ with the diagonal. The intersection point $(0, 0)$ (i.e. the diagonal point corresponding to the monomorphic trait value $\tau = 0$) is the rest point for the monomorphic dynamics (but not necessarily for adaptive dynamics as a whole due to the rare but ongoing occurrence of successful mutants, as in this specific configuration as we shall soon derive), and in the Figure is indicated by the black dot on the main diagonal. The two arrows on the main diagonal indicate the directions of monomorphic adaptive dynamics in these two sections. In the section of points $(\tau, \tau)$ with $\tau < 0$ the direction is upwards. Here only a mutant population with trait value $\nu > \tau$ is able to invade (as follows from the corresponding PIP in Figure 5.2). If such a $\nu$ is sufficiently close to $\tau$ then its invasion causes a trait substitution: the density of the mutant population increases and reaches a stable equilibrium on which the resident $\tau$-population is replaced by the mutant population. For points $(\tau, \tau)$ with $\tau > 0$ the monomorphic direction is downwards: here the $\tau$-population gets replaced by an invading mutant population whose trait $\nu$ is sufficiently close to $\tau$ and satisfies $\nu < \tau$. Monomorphic dynamics for this specific $s_1$-function therefore is directed towards the rest point $\tau = 0$. Trait values $\tau$ and $\nu$ both sufficiently close to 0 which satisfy $s_1(\tau, \nu) > 0$ and $s_1(\nu, \tau) > 0$ are mutually invadable. For such $\tau$ and $\nu$, invasion of the monomorphic $\tau$-population by the $\nu$-mutant population leads to coexistence on the $c$-attractor $\langle \tau, \nu \rangle$, and results in a trait increment. The adaptive dynamics then leaves $\mathbb{A}_1$ and enters $\mathbb{A}_2$. Once in $\mathbb{A}_2$, the dimorphic dynamics is directed away from the monomorphic rest point, as can be seen from the two arrows in $\mathbb{A}_2$ close to the monomorphic singularity. These arrows indicate the directions of dimorphic dynamics due to mutations in either one of the two traits present at elements of $\mathbb{A}_2$. In this specific configuration the direction of trait dynamics sustains on the evolutionary timescale, and evolutionary branching occurs. (How the directions of these arrows can be derived will soon be discussed.)

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

In $\mathbb{A}_2$ the two solid curves together form the so-called 1-isocline. The points $(\tau, \nu)$ on these curves are rest points for the 1-AD, and the 1-AD generically changes direction at the 1-isocline. The dotted curves compose the 2-isocline, and consist of the rest points of the 2-AD, at which 2-AD generically changes direction. The 1- and 2-isoclines divide the part of $\mathbb{A}_2$ above the main diagonal in four sections, and in each section the directions of adaptive dynamics due to a mutation in either the $\tau$- or $\nu$-trait have been indicated. Note that a rest point for the 1-AD or 2-AD generically is not a rest point for the adaptive dynamics as a whole; this is only the case in an intersection point of the 1- and 2-isocline. Rest points for the 1-AD may be locally attracting or repelling for the 1-AD, and a similar statement holds for rest points for the 2-AD. In Figure 5.3 all rest points on the 1-isocline as well as on the 2-isocline are locally attracting for their respective adaptive dynamics. At points within specific regions of either the 1- or the 2-isocline in $\mathbb{A}_2$ an increment in the number of trait values present may occur due to the entering into $\mathbb{A}_3$. Depending on the configuration of the local adaptive dynamics in $\mathbb{A}_3$, this may or may not lead to evolutionary branching from $\mathbb{A}_2$ into $\mathbb{A}_3$.

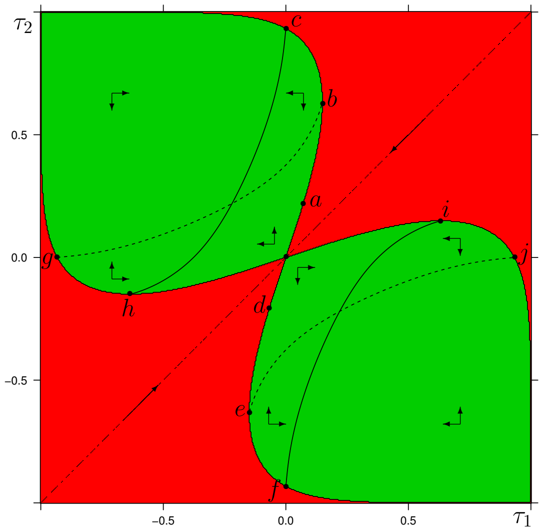

Figure 5.3: The TEP for the function $s_1(\tau;\nu) = 1 - \nu^2 - \dfrac{e^{-3(\tau-\nu)^2}}{1-0.5\nu^2}(1-0.5\tau^2)(1-\tau^2)$ on $[-1,1]^2$. (The PIP in Figure 5.2 and the MIP in Figure 5.1 are also based on this function $s_1$.) The arrows on the main diagonal, i.e., $\mathbb{A}_1$, indicate the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

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

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

### *Monomorphic dynamics*

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

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

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

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

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

From the expression

$$s_1(\tau;\nu) = (\nu - \tau)z_1(\tau;\nu), \tag{5.23}$$

with

$$z_1 : \mathbb{T}^2 \to \mathbb{R}, \tag{5.24}$$

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

*Dimorphic invasion fitness gradients*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

In point $a$, $\Gamma_1(\tau_1, \tau_2) < 0$, and in point $d$ $\Gamma_1(\tau_1, \tau_2) > 0$. From continuity arguments it then follows that for either of these points there exists a neighbourhood in $\mathbb{A}_2$ in which the 1-invasion fitness gradient at each point inherits the sign of $\Gamma(\tau_1)$. This neighbourhood is bounded by the 1-isocline, and on passing through this isocline the 1-invasion fitness gradient generically switches sign. Furthermore, in *a* $\Gamma_2(\tau_1, \tau_2) > 0$, because the function $\tau \mapsto s_1(\tau_1; \tau)$ is increasing on a neighbourhood of $\tau_2$. (We assume here the absence of the non-generic case of inflection at $\tau = \tau_2$.) Similarly, $(\tau_1, \tau_2)$ then has a neighbourhood in $\mathbb{A}_2$ in which the 2-isocline is positive, and this neighbourhood is bounded by the 2-isocline. By the same argument, point *d* has a neighbourhood in $\mathbb{A}_2$ in which the 2-isocline is negative.

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

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

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

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

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

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

### *Classifying monomorphic singularities*

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

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

we then may write

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

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

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

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

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

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

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

$$s_{0,2} < 0. \tag{5.33}$$

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

$$s_{2,0} > s_{0,2}. \tag{5.34}$$

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

$$s_{2,0} > s_{0,2} > 0 \tag{5.35}$$

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

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

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

In all the other cases where there is a region of coexistence attached to the monomorphic singularity, evolution in both the monomorphic as well as the dimorphic case is away from the singularity. Adaptive dynamics thus models the evolutionary process of the regular replacement of phenotypic trait values, possibly interspersed with evolutionary branching and pruning events. In the latter case, when plotted against evolutionary time the occurring trait values take the characteristic shape of a tree (see Figure 1.1).

**Remark 8.**

1. Note that in i.a. the case that $\mathbb{A}_2$ is not attached to $\mathbb{A}_1$ (which is the case if $s_1$ changes sign everywhere on the main diagonal in $\mathbb{A}_1 \times \mathbb{A}_1$, as in the PIP in Figure 5.5), it may occur that a dimorphic coalition by evolutionary dynamics is driven towards the boundary of $\mathbb{A}_2$. Close to the boundary a sufficiently large (but still small) mutation may cause the coalition to become monomorphic. Since in this case stepping back from $\mathbb{A}_1$ into $\mathbb{A}_2$ cannot happen under small mutational steps, trait evolution will proceed in $\mathbb{A}_1$, i.e., evolutionary pruning occurs. In case subsequent mutations in $\mathbb{A}_2$ drive the adaptive dynamics to the 2-isocline (in the upper left part of $\mathbb{A}_2$ in Figure 5.5(*b*)), it depends on the local dynamics at the 2-isocline how the evolutionary process will proceed: a mutation in the 1-trait will bring the dynamics closer to the boundary of $\mathbb{A}_2$, and thus to pruning, whereas a mutation in the 2-trait may possibly cause evolutionary branching to occur (although this is excluded in a neighbourhood of either one of the endpoints $(\tau_1, \tau_2)$ of the 2-isocline, since in such a point $s_2(\tau_1, \tau_2; \nu) < 0$ for a mutant trait $\nu$ generated by $\tau_2$).

2. The case where evolution in $\mathbb{A}_2$ is towards the monomorphic singularity and evolution in $\mathbb{A}_1$ is away from that singularity requires a TEP that in our framework is excluded by the condition on non-self-intersection of the zero set of the function $z_1$ in $(0,0)$. Figure 5.6 shows a configuration of a TEP that allows for this scenario, with $s_1(\tau;\nu) = (\nu - \tau)(\nu + 0.8\tau)(\nu + 4\tau)$. In the left upper part of $\mathbb{A}_2$, sufficiently close to the monomorphic singularity a mutation in either the $\tau_1$- or $\tau_2$-population will cause the community to become monomorphic, and subsequent mutations will cause a dynamics in the upwards direction in $\mathbb{A}_1$ (possibly first passing through the monomorphic singularity, depending on where the monomorphic dynamics starts). Note that the singularity in this configuration is unstable with respect to small perturbations: generically a small perturbation will result in a dynamics in the neighbourhood of a singularity that resembles one for a non-self-

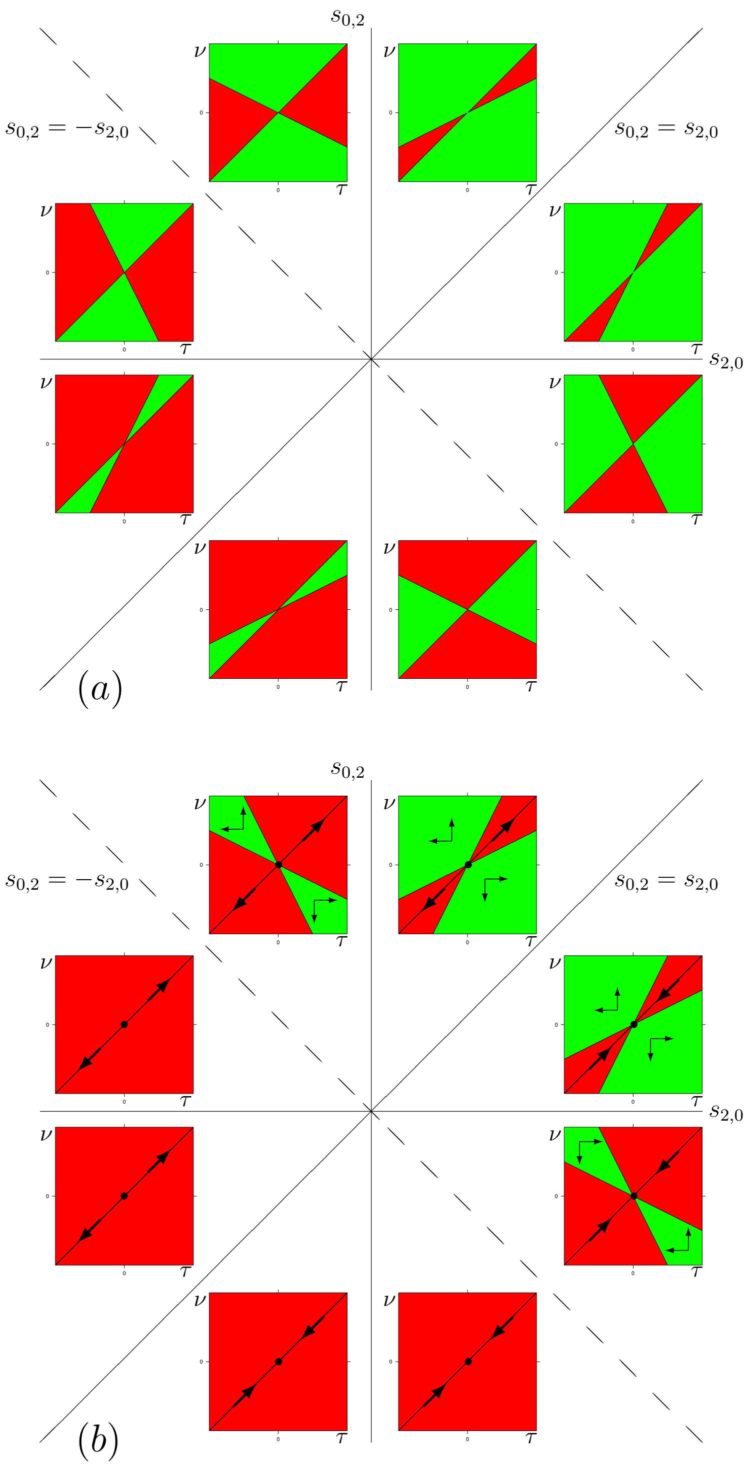
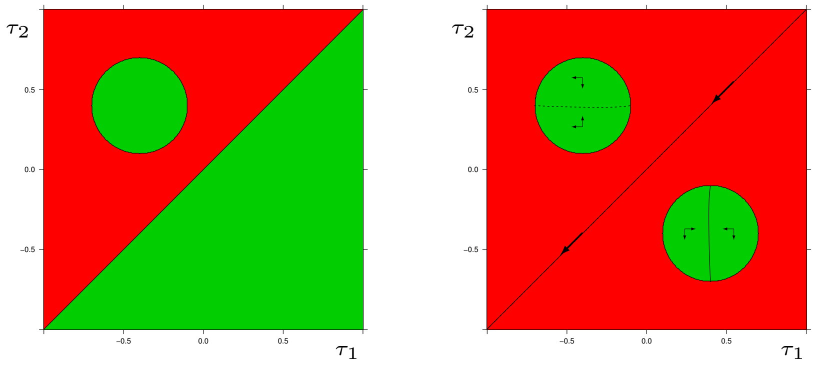


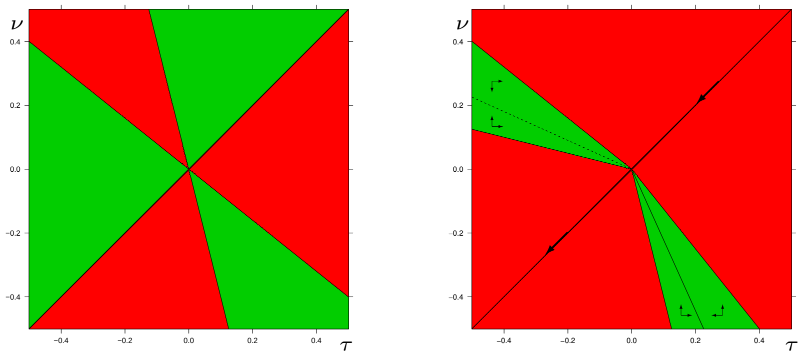
Figure 5.4: The classification of PIPs $(a)$ and TEPS $(b)$ in a sufficiently small neighbourhood of an ess in terms of $s_{2,0}$ and $s_{0,2}$ in case both $s_{2,0} \neq 0$ and $s_{0,2} \neq 0$, and furthermore $s_{2,0} \pm s_{0,2} \neq 0$ holds.



$(a)$ $(b)$

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

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



$(a)$ $(b)$

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

Since a TEP is determined by $z_1$, which in turn depends on the functions $r$ and $a$, a change of parameters in these functions generically will cause a change in the regions of coexistence. It thus may happen due to a change in parameters that a coalition goes extinct, or that an lESS turns into an invadable singularity. The evolutionary implications of parameter changes at a monomorphic singularity are studied in the bifurcation analysis paper [54].

*Dimorphic and trimorphic dynamics*

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

$$s_2(\tau_1, \tau_2; \nu) = (\nu - \tau_1)(\nu - \tau_2) z_2(\tau_1, \tau_2; \nu), \tag{5.36}$$

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

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

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

and

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

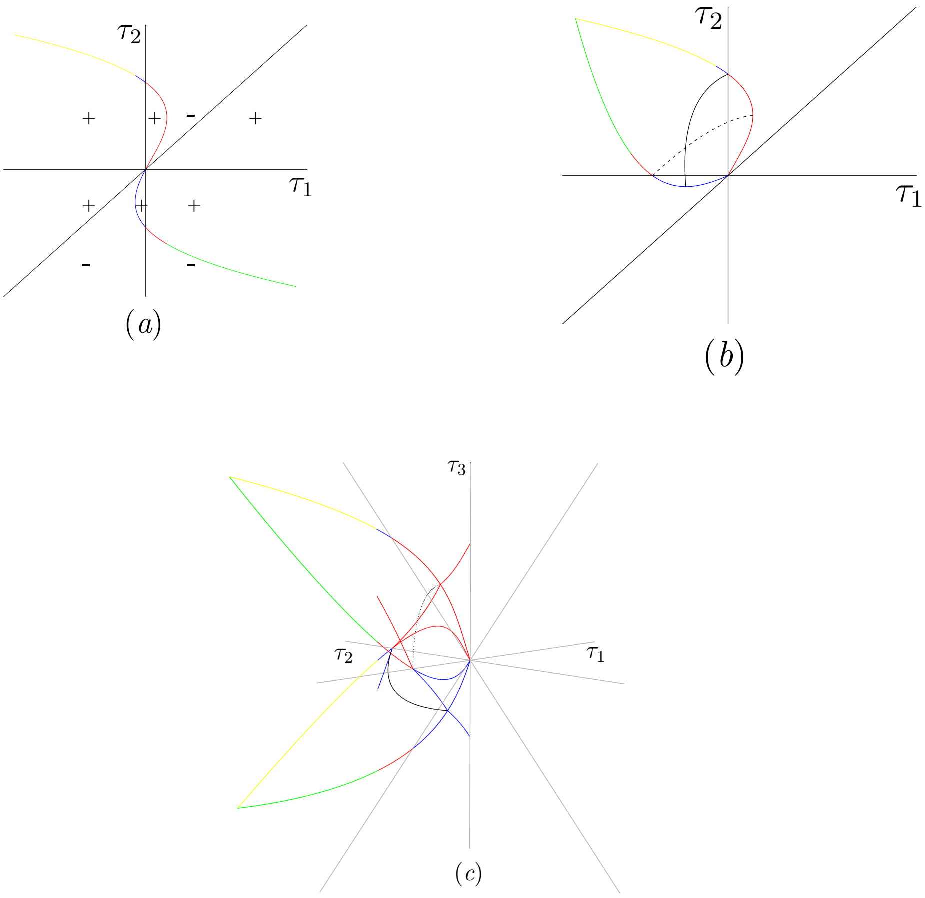
Therefore, at a point $(\tau_1, \tau_2, \tau_1) \in \triangle^3_{1,3}$ (with $\tau_1 < \tau_2$) the gradient $\Gamma_1(\tau_1, \tau_2)$ is positive (negative) if and only if $z_2(\tau_1, \tau_2; \tau_1)$ is negative (positive). Similarly, at a point $(\tau_1, \tau_2, \tau_2) \in \triangle^3_{2,3}$ the gradient $\Gamma_2(\tau_1, \tau_2)$ is positive (negative) if and only if $z_2(\tau_1, \tau_2; \tau_2)$ is positive (negative). A trait substitution due to a mutation in the 1-trait then corresponds to a step in the 1-direction (or, more precisely, in the $1,3$-direction, i.e., the direction of the vector $(1,0,1)$ in $\mathbb{T}^3$) in the embedding of $\mathbb{A}_2$ in $\triangle^3_{1,3}$, in a process similar to stepping along the diagonal $\triangle^2_{1,2}$ due to trait substitutions in the embedded $\mathbb{A}_1$. A trait substitution in the 2-trait corresponds to a step in the $2,3$- or $(0,1,1)$-direction in the embedding of $\mathbb{A}_2$ in $\triangle^3_{2,3}$. The evolutionary path followed by the dimorphic community in $\mathbb{A}_2$ then can be represented in two ways: in $\triangle^3_{1,3}$ as well as in $\triangle^3_{2,3}$. A trait substitution $\langle \tau_1, \tau_2 \rangle \to \langle \tau_1', \tau_2 \rangle$ is represented in $\triangle^3_{1,3}$ by stepping from $(\tau_1, \tau_2, \tau_1)$ to $(\tau_1', \tau_2, \tau_1')$, and in $\triangle^3_{2,3}$ by stepping from $(\tau_1, \tau_2, \tau_2)$ to $(\tau_1', \tau_2, \tau_2)$. Similarly, the trait substitution $\langle \tau_1, \tau_2 \rangle \to \langle \tau_1, \tau_2' \rangle$ in $\triangle^3_{1,3}$ is indicated by the change from $(\tau_1, \tau_2, \tau_1)$ into $(\tau_1, \tau_2', \tau_1)$, and in $\triangle^3_{2,3}$ by the change from $(\tau_1, \tau_2, \tau_2)$ into $(\tau_1, \tau_2', \tau_2')$.

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

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

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

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



$(a)$

$(b)$

$(c)$

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

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

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

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

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

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

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

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

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

$$C_{2,3}(\tau_1, \tau_2) \;=\; \{(\tau_1, \tau_2 + \tau, \tau_2 + \nu) | \tau, \nu \;\; \textit{such that}\; \tau_1 + \tau, \tau_1 + \nu \;\in\; \mathbb{T}\}, \tag{5.42}$$

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

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

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

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

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

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

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

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

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

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

## 5.3 ADAPTIVE DYNAMICS: THE MATHEMATICAL FRAMEWORK

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

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

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

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

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

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

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

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

Together with the definition of $s_0$ (Definition 4), we thus have defined $s_k : R(\mathbb{T}^k) \times \mathbb{T} \to \mathbb{R}$ for any $k \geq 0$. The mathematical properties of the invasion fitness functions derived in the previous section in case $k \geq 1$ extend straightforwardly to the functions $s_k$ for all $(\tau_1, \ldots, \tau_k) \in R(\mathbb{T}^k)$ (with the exception, already mentioned above, that now $\hat{x}(\tau_1, \ldots, \tau_k)$ does not have to belong to the interior of the community state space). In particular we have for each $(\tau_1, \dots, \tau_k) \in R(\mathbb{T}^k)$ and for all $i \in \{1, \dots, k\}$ that $s_k(\tau_1, \dots, \tau_k; \tau_i) = 0$ (see also Remark 9 below). For any permutation $\sigma \in \Sigma_k$: $s_k(\tau_1, \dots, \tau_k; \nu) = s_k(\tau_{\sigma(1)}, \dots, \tau_{\sigma(k)}; \nu)$. Furthermore, for any $k, l \in \mathbb{N}$, $l \leq k$ and $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ a subset of distinct elements such that $(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in R(\mathbb{T}^{k-l})$, the notation $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \nu)$ makes sense.

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

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

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

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

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

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

The functions $s_k$ are now further generalised.

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

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

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

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

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

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

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

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

$$S_k(\tau_1, \ldots, \tau_k; \nu) = |F_k(\tau_1, \ldots, \tau_k; \nu)|. \tag{5.46}$$

In addition we define $S_0 = s_0$.

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

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

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

1. The functions $S_k$ inherit the differentiability properties of the functions $r$ and $a$.
2. For all $\sigma \in \Sigma_k$: $S_k(\tau_1, \ldots, \tau_k; \nu) = S_k(\tau_{\sigma(1)}, \ldots, \tau_{\sigma(k)}; \nu)$.
3. $$S_k(\tau_1, \ldots, \tau_k; \nu) \;=\; r(\nu)|A(\tau_1, \ldots, \tau_k)| - \sum_{i=1}^{k} a(\nu, \tau_i) S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i). \tag{5.47}$$
4. For each $i \in \{1, \ldots, k\}$: $S_k(\tau_1, \ldots, \tau_k; \tau_i) = 0$, and consequently $$r(\tau_i)|A(\tau_1, \ldots, \tau_k)| = \sum_{j=1}^{k} a(\tau_i, \tau_j) S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_j). \tag{5.48}$$
5. If $(\tau_1, \ldots, \tau_k) \in \triangle^k$, then for all $\nu \in \mathbb{T}$: $S_k(\tau_1, \ldots, \tau_k; \nu) = 0$.
6. If for all $i \in \{1, \ldots, k\}$: $S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i) = 0$, and for at least one $j \in \{1, \ldots, k\}$: $r(\tau_j) \neq 0$, then $|A(\tau_1, \ldots, \tau_k)| = 0$, and consequently for all $\nu \in \mathbb{T}$: $S_k(\tau_1, \ldots, \tau_k; \nu) = 0$.

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

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

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

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

satisfies:

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

Consequently,

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

2. $$S_k(\tau_1, \dots, \tau_k; \nu) = |A(\tau_1, \dots, \tau_k)| s_k(\tau_1, \dots, \tau_k; \nu). \tag{5.51}$$

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

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

As a consequence of expression (5.52) we now can also extend the notion of invasion fitness gradient from $\mathbb{A}_k$ to $R(\mathbb{T}^k)$: for $(\tau_1, \dots, \tau_k)$, and for $i = 1, \dots, k$, the $i$-invasion fitness gradient $\Gamma_i(\tau_1,\dots,\tau_k)$ equals $\partial_{0,\dots,0,1}s_k(\tau_1,\dots,\tau_k;\tau_i)$. In $R(\mathbb{T}^k)$, the $i$-isocline then is defined as to consist of those $(\tau_1,\dots,\tau_k) \in R(\mathbb{T}^k)$ for which $\Gamma_i(\tau_1,\dots,\tau_k)$ equals 0.

Lemma 5 implies

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

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

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

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

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

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

At the end of the first part of this paper we argued that the adaptive-dynamical scenario that occurs due to the generation of mutants by population $i$ on an attractor $\langle\tau_1,\dots,\tau_k\rangle$ on the $i$-isocline depends on the local configuration of the zero set of the function $z_k$ at $(\tau_1,\dots,\tau_k,\tau_i) \in \triangle^{k+1}_{i,k+1}$. The Corollary shows that necessary conditions for the coexistence of mutants and residents are obtained from the mutual invasion fitnesses $s_k(\tau_1,\dots,\tau_k;\tau_{k+1})$ and $s_k(\tau_1,\dots,\tau_k,\tau_{k+1}\setminus\tau_i;\tau_i)$ in the $C_{i,k+1}(\tau_1,\dots,\tau_{k+1})$-slice. These conditions have to be combined with conditions on the signs of the determinants $|A(\tau_1,\dots,\tau_{k+1})|$ and $|A(\tau_1,\dots,\tau_{k+1}\setminus\tau_j)|$, and conditions on the signs of the expressions $s_k(\tau_1,\dots,\tau_{k+1}\setminus\tau_j;\tau_j)$, with $j\in\{1,\dots,k\}\setminus\{i\}$. For these values of $j$ the points $(\tau_1,\dots,\tau_{k+1}\setminus\tau_j)$ as well as $(\tau_1,\dots,\tau_{k+1})$ lie close to diagonal hyperplanes, on which the determinants become 0 and on which $s_k(\tau_1,\dots,\tau_{k+1}\setminus\tau_j;\tau_j)$ is not defined. In the next subsection we shall derive the required signs by means of Lemma 7, that we state after the following Example.

**Example 3.**

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

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

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

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

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

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

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

**Lemma 7.**

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

$$|A(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_l})| \; S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i) -$$

$$|A(\tau_1, \ldots, \tau_k)| \; S_{k-l-1}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_l}, \tau_i; \tau_i) \;=$$

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

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

$$|A(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_l})| \; S_k(\tau_1, \ldots, \tau_k; \tau_{k+1}) -$$

$$|A(\tau_1, \ldots, \tau_k)| \; S_{k-l}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_l}; \tau_{k+1}) \;=$$

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

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

$$\frac{S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i)}{|A(\tau_1, \ldots, \tau_k)|} - \frac{S_{k-l-1}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_l}, \tau_i; \tau_i)}{|A(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_l})|} \;=$$

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

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

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

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

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

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

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

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

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

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

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

and

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

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

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

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

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

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

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

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

1. for all $j = 1, \dots, k-1$: $\hat{x}_j(\tau_1, \dots, \tau_{k+1}) > 0$, i.e.
$$\frac{S_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_j; \tau_j)}{|A(\tau_1, \dots, \tau_{k+1})|} < 0; \tag{5.62}$$
2.
$$s_k(\tau_1, \dots, \tau_{k+1} \setminus \tau_k; \tau_k) > 0; \tag{5.63}$$
3.
$$\operatorname{sign}(|A(\tau_1, \dots, , \tau_k, \tau_{k+1})|) = -\operatorname{sign}(|A(\tau_1, \dots, \tau_k)|). \tag{5.64}$$

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

**Lemma 9.**

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

The proof of this Lemma is given in Appendix 5.5.3

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

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

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

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

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

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

$$\operatorname{sign}\big(\partial_{0,\ldots,0,1}S_{k-1}(\tau_1,\ldots,\tau_k \setminus \tau_j;\tau_k)\big) =$$

$$-\operatorname{sign}\Big((-1)^{j-k}\frac{d|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k}\Big). \tag{5.65}$$

2. Let $j \in \{1,\ldots,k-1\}$. Let in addition $\partial_{0,\ldots,0,2}s_k(\tau_1,\ldots,\tau_k;\tau_k) + \partial_{0,\ldots,0,2,0}s_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) > 0$ hold. Then

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

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

**Corollary 8.** Let $k \geq 1$ and let $\langle \tau_1,\ldots,\tau_k \rangle \in \mathbb{A}_k$ belong to the $i$-isocline. Suppose a mutant population with phenotypic trait value $\nu = \tau_{k+1}$ emerges from population $i$ with positive fitness. If both $\partial_{0,\ldots,0,2,0,\ldots,0}s_k(\tau_1,\ldots,\tau_{i-1},\tau_i,\tau_{i+1},\ldots,\tau_k;\tau_i) > 0$ and $\partial_{0,\ldots,0,2}s_k(\tau_1,\ldots,\tau_k;\tau_i) > 0$ hold, then for $\tau_{k+1}$ sufficiently close to $\tau_i$ the conditions mentioned in Corollary 7 necessary for invasion to lead to coexistence on $\langle \tau_1,\ldots,\tau_k,\tau_{k+1} \rangle \in \mathbb{A}_{k+1}$ are satisfied.

### 5.3.3 *Permanence*

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

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

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

with summation over all boundary rest points $x$.

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

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

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

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

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

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

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

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

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

holds.

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

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

A proof of this Lemma is given in Appendix 5.5.6

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

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

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

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

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

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

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

1. An evolutionary path which starts in a trait combination whose corresponding Lotka-Volterra model is $s$-permanent and which consists of sufficiently small mutational steps will end in a $s$-permanent Lotka-Volterra model.

2. To reach a non-$s$-permanent Lotka-Volterra model from a $s$-permanent Lotka-Volterra model by means of a sequence of mutational steps requires at least one sufficiently large mutational step.

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

## 5.4 DISCUSSION

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

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

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

Although we restricted ourselves to scalar phenotypic traits, various results also hold for trait vectors. In particular we may in expression (5.61) substitute trait vectors instead of scalars for the various symbols $\tau_i$, $i = 1, \ldots, k$ and $\nu$, and it easily follows that the necessary conditions (5.62), (5.63) and (5.64) must be satisfied for invasion to lead to coexistence of the mutant population with all resident populations in case of trait vectors. Expressions and results that involve differentiation are however restricted to scalar traits. In case of trait vectors the invasion fitness function can be obtained as a matrix expression, and in a sufficiently small neighbourhood of a singular trait vector adaptive-dynamical properties can be characterised in terms of matrix properties, see e.g. [41].

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

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

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

## 5.5 APPENDICES

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

### 5.5.1 *Proof of Lemma 7*

#### 5.5.1.1 *Proof of Lemma 7.1*

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

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

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

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

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

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

In the last column in the matrix in this expression, the element in the $j$-th row by means of (5.47) equals $S_{k-l}(\tau_1,\ldots,\tau_k \setminus \tau_{j_1},\ldots,\tau_{j_l};\tau_j) + \sum_{\substack{\alpha=1 \\ \alpha\neq j_1,\ldots,j_l,i}}^{k} a(\tau_j,\tau_\alpha)\; S_{k-l-1}(\tau_1,\ldots,\tau_k \setminus \tau_{j_1},\ldots,\tau_{j_l},\tau_\alpha;\tau_\alpha)$, and so the previous expression equals

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

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

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

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

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

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

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

### 5.5.1.2 *Proof of Lemma 7.2*

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

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

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

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

### 5.5.2 *Proof of Lemma 8*

The denominator in the right hand side of expression (5.61), $\left|\begin{pmatrix} 0 & s_1(\tau_1;\tau_2) & \cdot & \cdot & s_1(\tau_1;\tau_k) & 1 \\ s_1(\tau_2;\tau_1) & 0 & \cdot & \cdot & s_1(\tau_2;\tau_k) & 1 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k;\tau_1) & s_1(\tau_k;\tau_2) & \cdot & \cdot & 0 & 1 \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & 1 \end{pmatrix}\right|$, can be rewritten by subtracting the last row from each of the other rows in the matrix. This yields the following determinant:

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

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

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

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

$$\left|\begin{pmatrix} 0 & s_1(\tau_1;\tau_2) & \cdot & \cdot & s_1(\tau_1;\tau_{k-1}) & s_1(\tau_1;\nu) \\ s_1(\tau_2;\tau_1) & 0 & \cdot & \cdot & s_1(\tau_2;\tau_{k-1}) & s_1(\tau_2;\nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_{k-1};\tau_1) & s_1(\tau_{k-1};\tau_2) & \cdot & \cdot & 0 & s_1(\tau_{k-1};\nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_{k-1}) & r(\nu) \end{pmatrix}\right| = (-1)^{k-1}S_{k-1}(\tau_1,\ldots,\tau_{k-1};\nu)\prod_{i=1}^{k-1}\frac{r(\tau_i)}{a(\tau_i,\tau_i)}.$$

The numerator of (5.61), $\left|\begin{pmatrix} 0 & s_1(\tau_1;\tau_2) & \cdot & \cdot & s_1(\tau_1;\tau_k) & s_1(\tau_1;\nu) \\ s_1(\tau_2;\tau_1) & 0 & \cdot & \cdot & s_1(\tau_2;\tau_k) & s_1(\tau_2;\nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k;\tau_1) & s_1(\tau_k;\tau_2) & \cdot & \cdot & 0 & s_1(\tau_k;\nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix}\right|$, then is equal to

$$\left|\begin{pmatrix} 0 & s_1(\tau_1;\tau_2) & \cdot & \cdot & s_1(\tau_1;\tau_k) & r(\nu)-a(\nu,\tau_1)\dfrac{r(\tau_1)}{a(\tau_1,\tau_1)} \\ s_1(\tau_2;\tau_1) & 0 & \cdot & \cdot & s_1(\tau_2;\tau_k) & r(\nu)-a(\nu,\tau_2)\dfrac{r(\tau_2)}{a(\tau_2,\tau_2)} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k;\tau_1) & s_1(\tau_k;\tau_2) & \cdot & \cdot & 0 & r(\nu)-a(\nu,\tau_k)\dfrac{r(\tau_k)}{a(\tau_k,\tau_k)} \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix}\right| =$$

$$\left|\begin{pmatrix} 0 & s_1(\tau_1;\tau_2) & \cdot & \cdot & s_1(\tau_1;\tau_k) & r(\nu) \\ s_1(\tau_2;\tau_1) & 0 & \cdot & \cdot & s_1(\tau_2;\tau_k) & r(\nu) \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k;\tau_1) & s_1(\tau_k;\tau_2) & \cdot & \cdot & 0 & r(\nu) \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & r(\nu) \end{pmatrix}\right| + \left|\begin{pmatrix} 0 & s_1(\tau_1;\tau_2) & \cdot & \cdot & s_1(\tau_1;\tau_k) & -a(\nu,\tau_1)\dfrac{r(\tau_1)}{a(\tau_1,\tau_1)} \\ s_1(\tau_2;\tau_1) & 0 & \cdot & \cdot & s_1(\tau_2;\tau_k) & -a(\nu,\tau_2)\dfrac{r(\tau_2)}{a(\tau_2,\tau_2)} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ s_1(\tau_k;\tau_1) & s_1(\tau_k;\tau_2) & \cdot & \cdot & 0 & -a(\nu,\tau_k)\dfrac{r(\tau_k)}{a(\tau_k,\tau_k)} \\ r(\tau_1) & r(\tau_2) & \cdot & \cdot & r(\tau_k) & 0 \end{pmatrix}\right|. \qquad (5.71)$$

The first of the last two determinants equals $r(\nu)$ × (the denominator), and therefore by (5.70) is equal to $(-1)^k r(\nu)|A(\tau_1,\ldots,\tau_k)|\prod_{i=1}^{k}\dfrac{r(\tau_i)}{a(\tau_i,\tau_i)}$. The second determinant in the last expression by the induction hypothesis equals

$$\sum_{i=1}^{k}(-1)^{k+i}a(\nu,\tau_i)\frac{r(\tau_i)}{a(\tau_i,\tau_i)}(-1)^{k-i}(-1)^{k-1}S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_i;\tau_i)\prod_{\substack{j=1\\ j\neq i}}^{k}\frac{r(\tau_j)}{a(\tau_j,\tau_j)} =$$
$$(-1)^{k-1}\sum_{i=1}^{k}a(\nu,\tau_i)S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_i;\tau_i)\prod_{j=1}^{k}\frac{r(\tau_j)}{a(\tau_j,\tau_j)}.$$

With (5.71) it then follows that the numerator of (5.61) equals

$$(-1)^k\prod_{j=1}^{k}\frac{r(\tau_j)}{a(\tau_j,\tau_j)}\left(r(\nu)|A(\tau_1,\ldots,\tau_k)|-\sum_{i=1}^{k}a(\nu,\tau_i)S_{(\tau_1,\ldots,\tau_k\setminus\tau_i)}(\tau_i)\right),$$

which by (5.47) is equal to $(-1)^k S_k(\tau_1,\ldots,\tau_k;\nu)\prod_{j=1}^{k}\frac{r(\tau_j)}{a(\tau_j,\tau_j)}$. This result together with expressions (5.70) for the denominator and (5.51) in Lemma 5 now yield the validity of the statement for the case that all $r(\tau_i)\neq 0$. By applying l'Hôpital's argument the result can be extended to cases in which $(\tau_1,\ldots,\tau_k)$ is such that $r$ has isolated zeros at on or more of the $\tau_i$, $i=1,\ldots,k$.

### 5.5.3 *Proof of Lemma 9*

#### 5.5.3.1 *Proof of Lemma 9.1*

Let $D_i(A(\tau_1,\ldots,\tau_k,\tau_k))$ denote the matrix obtained by differentiating each element in the $i$-th column of $A(\tau_1,\ldots,\tau_{k+1})$ with respect to $\tau_{k+1}$, and subsequently taking $\tau_{k+1}=\tau_k$. Then for $i=1,\ldots,k-1$, the determinant $|D_i(A(\tau_1,\ldots,\tau_k,\tau_k))|=0$, since the $k$-th and $k+1$-th column in $D_i(A(\tau_1,\ldots,\tau_k,\tau_k))$ are equal. Therefore

$$\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_k,\tau_k)| = |D_k(A(\tau_1,\ldots,\tau_k,\tau_k))| + |D_{k+1}(A(\tau_1,\ldots,\tau_k,\tau_k))|,$$

with

$$|D_k(A(\tau_1,\ldots,\tau_k,\tau_k))| = \left|\begin{pmatrix} a(\tau_1,\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_1,\tau_{k-1}) & 0 & a(\tau_1,\tau_k) \\ \cdot & \cdot\;\cdot\;\cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot\;\cdot\;\cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot\;\cdot\;\cdot & \cdot & \cdot & \cdot \\ a(\tau_{k-1},\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_{k-1},\tau_{k-1}) & 0 & a(\tau_{k-1},\tau_k) \\ a(\tau_k,\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_k,\tau_{k-1}) & 0 & a(\tau_k,\tau_k) \\ a(\tau_k,\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_k,\tau_{k-1}) & \partial_{1,0}a(\tau_k,\tau_k) & a(\tau_k,\tau_k) \end{pmatrix}\right|, \tag{5.72}$$

and

$$|D_{k+1}(A(\tau_1,\ldots,\tau_k,\tau_k))| = \left|\begin{pmatrix} a(\tau_1,\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_1,\tau_{k-1}) & a(\tau_1,\tau_k) & \partial_{0,1}a(\tau_1,\tau_k) \\ \cdot & \cdot\;\cdot\;\cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot\;\cdot\;\cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot\;\cdot\;\cdot & \cdot & \cdot & \cdot \\ a(\tau_{k-1},\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_{k-1},\tau_{k-1}) & a(\tau_{k-1},\tau_k) & \partial_{0,1}a(\tau_{k-1},\tau_k) \\ a(\tau_k,\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_k,\tau_{k-1}) & a(\tau_k,\tau_k) & \partial_{0,1}a(\tau_k,\tau_k) \\ a(\tau_k,\tau_1) & \cdot\;\cdot\;\cdot & a(\tau_k,\tau_{k-1}) & a(\tau_k,\tau_k) & \partial_{1,0}a(\tau_k,\tau_k)+\partial_{0,1}a(\tau_k,\tau_k) \end{pmatrix}\right|. \tag{5.73}$$

Exchanging the two last columns in the matrix of (5.72) yields a matrix whose first $k$ columns are equal to that in the matrix in (5.73), and whose determinant equals $-|D_k(A(\tau_1,\ldots,\tau_k,\tau_k))|$. So $\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_k,\tau_k)|$ equals

$$\left|\begin{pmatrix} a(\tau_1,\tau_1) & \cdot\ \cdot\ \cdot & a(\tau_1,\tau_{k-1}) & a(\tau_1,\tau_k) & \partial_{0,1}a(\tau_1,\tau_k) \\ \cdot & \cdot\ \cdot\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot\ \cdot\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot\ \cdot\ \cdot & \cdot & \cdot & \cdot \\ a(\tau_{k-1},\tau_1) & \cdot\ \cdot\ \cdot & a(\tau_{k-1},\tau_{k-1}) & a(\tau_{k-1},\tau_k) & \partial_{0,1}a(\tau_{k-1},\tau_k) \\ a(\tau_k,\tau_1) & \cdot\ \cdot\ \cdot & a(\tau_k,\tau_{k-1}) & a(\tau_k,\tau_k) & \partial_{0,1}a(\tau_k,\tau_k) \\ a(\tau_k,\tau_1) & \cdot\ \cdot\ \cdot & a(\tau_k,\tau_{k-1}) & a(\tau_k,\tau_k) & \partial_{0,1}a(\tau_k,\tau_k) \end{pmatrix}\right| = 0, \tag{5.74}$$

since the last two rows in the matrix are equal.

### 5.5.3.2 *Proof of Lemma 9.2*

In (5.56) we replace $k$ by $k+1$, set $l$ equal to 1 and take $j_1 = k$, and take $i$ equal to $k+1$. We then obtain that

$$|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_k)|\ S_k(\tau_1,\ldots,\tau_k;\tau_{k+1})\ -\ |A(\tau_1,\ldots,\tau_{k+1})|\ S_{k-1}(\tau_1,\ldots,\tau_{k+1}\setminus\tau_k,\tau_{k+1};\tau_{k+1})\ =$$

$$-\ |A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|\ S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_k;\tau_k),$$

i.e.,

$$|A(\tau_1,\ldots,\tau_{k-1},\tau_{k+1})|\ S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) - |A(\tau_1,\ldots,\tau_{k+1})|\ S_{k-1}(\tau_1,\ldots,\tau_{k-1};\tau_{k+1}) =$$

$$-\ |A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|\ S_k(\tau_1,\ldots,\tau_{k-1},\tau_{k+1};\tau_k). \tag{5.75}$$

Differentiating the left- and right hand side of this expression with respect to $\tau_{k+1}$ yields

$$\partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_{k-1},\tau_{k+1})|\; S_k(\tau_1,\dots,\tau_k;\tau_{k+1}) \;+\; |A(\tau_1,\dots,\tau_{k-1},\tau_{k+1})|\;\partial_{0,\dots,0,1}S_k(\tau_1,\dots,\tau_k;\tau_{k+1}) \;-$$

$$\partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_{k+1})|\; S_{k-1}(\tau_1,\dots,\tau_{k-1};\tau_{k+1}) \;-\; |A(\tau_1,\dots,\tau_{k+1})|\;\partial_{0,\dots,0,1}S_{k-1}(\tau_1,\dots,\tau_{k-1};\tau_{k+1}) \;=$$

$$-\,\partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_{k+1})_{(k,k+1)}|\; S_k(\tau_1,\dots,\tau_{k-1},\tau_{k+1};\tau_k) \;-\; |A(\tau_1,\dots,\tau_{k+1})_{(k,k+1)}|\;\partial_{0,\dots,0,1,0}S_k(\tau_1,\dots,\tau_{k-1},\tau_{k+1};\tau_k).$$

Taking variable $\tau_{k+1}$ equal to $\tau_k$ makes $S_k(\tau_1,\dots,\tau_k;\tau_{k+1})$ as well as $S_k(\tau_1,\dots,\tau_{k-1},\tau_{k+1};\tau_k)$ equal to 0. Also, $|A(\tau_1,\dots,\tau_k,\tau_{k+1})|$ and, by the first part of the Lemma, $\partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_{k+1})|$ become 0. Furthermore, $|A(\tau_1,\dots,\tau_{k+1})_{(k,k+1)}|$ becomes equal to $|A(\tau_1,\dots,\tau_k)|$. We obtain that $|A(\tau_1,\dots,\tau_{k-1},\tau_k)|\;\partial_{0,\dots,0,1}S_k(\tau_1,\dots,\tau_k;\tau_k) \;=\; -\,|A(\tau_1,\dots,\tau_k)|\;\partial_{0,\dots,0,1,0}S_k(\tau_1,\dots,\tau_{k-1},\tau_k;\tau_k)$, which also follows from the fact that the function $\tau \mapsto S_k(\tau_1,\dots,\tau_{k-1},\tau;\tau)$ is identical to the zero function (Corollary 6, fourth statement), and therefore $\partial_{0,\dots,0,1,0}S_k(\tau_1,\dots,\tau_{k-1},\tau_k;\tau_k) \;+\; \partial_{0,\dots,0,1,0}S_k(\tau_1,\dots,\tau_{k-1},\tau_k;\tau_k) = 0$.

Differentiating the left- and right hand side of (5.75) twice with respect to $\tau_{k+1}$ yields

$$\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k-1},\tau_{k+1})|\; S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;+\; 2\,\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k-1},\tau_{k+1})|\; \partial_{0,\ldots,0,1}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;+$$

$$|A(\tau_1,\ldots,\tau_{k-1},\tau_{k+1})|\; \partial_{0,\ldots,0,2}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;-\; \partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k+1})|\; S_{k-1}(\tau_1,\ldots,\tau_{k-1};\tau_{k+1}) \;-$$

$$2\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k+1})|\; \partial_{0,\ldots,0,1}S_{k-1}(\tau_1,\ldots,\tau_{k-1};\tau_{k+1}) \;-\; |A(\tau_1,\ldots,\tau_{k+1})|\; \partial_{0,\ldots,0,2}S_{k-1}(\tau_1,\ldots,\tau_{k-1};\tau_{k+1}) \;=$$

$$-\,\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|\; S_k(\tau_1,\ldots,\tau_{k-1},\tau_{k+1};\tau_k) \;-$$

$$2\,\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|\; \partial_{0,\ldots,0,1,0}S_k(\tau_1,\ldots,\tau_{k-1},\tau_{k+1};\tau_k) \;-\; |A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|\; \partial_{0,\ldots,0,2,0}S_k(\tau_1,\ldots,\tau_{k-1},\tau_{k+1};\tau_k).$$

Again setting $\tau_{k+1}$ equal to $\tau_k$ and using $\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_k,\tau_k)| = 0$, we get the equality

$$2\,\frac{d|A(\tau_1,\ldots,\tau_{k-1},\tau_k)|}{d\tau_k}\; \partial_{0,\ldots,0,1}S_k(\tau_1,\ldots,\tau_k;\tau_k) \;+\; |A(\tau_1,\ldots,\tau_{k-1},\tau_k)|\; \partial_{0,\ldots,0,2}S_k(\tau_1,\ldots,\tau_k;\tau_k) \;-$$

$$\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_k,\tau_k)|\; S_{k-1}(\tau_1,\ldots,\tau_{k-1};\tau_k) \;=$$

$$-\,2\,\frac{d|A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k}\; \partial_{0,\ldots,0,1,0}S_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) \;-\; |A(\tau_1,\ldots,\tau_k)|\; \partial_{0,\ldots,0,2,0}S_k(\tau_1,\ldots,\tau_k;\tau_k).$$

Since $|A(\tau_1,\ldots,\tau_k)| \neq 0$ (because $\langle\tau_1,\ldots,\tau_k\rangle \in \mathbb{A}_k$) we may write (see (5.49)) $\hat{x}_k(\tau_1,\ldots,\tau_k) = -\dfrac{S_{k-1}(\tau_1,\ldots,\tau_{k-1};\tau_k)}{|A(\tau_1,\ldots,\tau_k)|}$. The previous expression then can be rewritten as

$$
\begin{aligned}
&-\frac{2}{|A(\tau_1,\ldots,\tau_k)|} \times \Big(\frac{d|A(\tau_1,\ldots,\tau_{k+1})_{(k,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k} \partial_{0,\ldots,0,1,0} S_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) + \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad \frac{d|A(\tau_1,\ldots,\tau_{k-1},\tau_k)|}{d\tau_k} \partial_{0,\ldots,0,1} S_k(\tau_1,\ldots,\tau_k;\tau_k)\Big) - \\
&\qquad \partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_k,\tau_k)|\, \hat{x}_k(\tau_1,\ldots,\tau_k) = \partial_{0,\ldots,0,2,0} S_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) + \partial_{0,\ldots,0,2} S_k(\tau_1,\ldots,\tau_k;\tau_k). \quad (5.76)
\end{aligned}
$$

Since (see (5.51)) $S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) = |A(\tau_1,\ldots,\tau_k)|\, s_k(\tau_1,\ldots,\tau_k;\tau_{k+1})$, and the function $\tau \mapsto S_k(\tau,\ldots,\tau_{k-1},\tau;\tau)$ equals the zero function, it follows, since $\langle\tau_1,\ldots,\tau_k\rangle$ belongs to the $k$-isocline, i.e., $\partial_{0,\ldots,0,1} s_k(\tau_1,\ldots,\tau_k;\tau_k) = 0$, that both $\partial_{0,\ldots,0,1} S_k(\tau_1,\ldots,\tau_k;\tau_k) = 0$ and $\partial_{0,\ldots,0,1,0} S_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) = 0$ hold. Furthermore, because by the first part of this Lemma $\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_k,\tau_k)| = 0$, the equality $\partial_{0,\ldots,0,2,0} S_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) = |A(\tau_1,\ldots,\tau_k)|\, \partial_{0,\ldots,0,2,0} s_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k)$ holds. Finally, $\partial_{0,\ldots,0,2} S_k(\tau_1,\ldots,\tau_k;\tau_k) = |A(\tau_1,\ldots,\tau_k)|\, \partial_{0,\ldots,0,2} s_k(\tau_1,\ldots,\tau_k;\tau_k)$. Equality (5.76) then becomes

$$
-\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_k,\tau_k)|\, \hat{x}_k(\tau_1,\ldots,\tau_k) = |A(\tau_1,\ldots,\tau_k)|\, \big(\partial_{0,\ldots,0,2,0} s_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) + \partial_{0,\ldots,0,2} s_k(\tau_1,\ldots,\tau_k;\tau_k)\big) \quad (5.77)
$$

Since by assumption both $\hat{x}_k(\tau_1,\ldots,\tau_k) > 0$ and $\partial_{0,\ldots,0,2,0} s_k(\tau_1,\ldots,\tau_{k-1},\tau_k;\tau_k) + \partial_{0,\ldots,0,2} s_k(\tau_1,\ldots,\tau_k;\tau_k) > 0$, it follows for values $\tau_{k+1}$ sufficiently close to $\tau_k$ that $\mathrm{sign}(|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|) = -\mathrm{sign}(|A(\tau_1,\ldots,\tau_k)|)$.

### 5.5.4 *Proof of Lemma 10*

The validity of the Lemma is derived by means of induction. We first prove that for $k = 2$ the equality $\partial_{0,1,0}S_2(\tau_1, \tau_1, \nu) = 0$ holds. By (5.47) we have that $S_2(\tau_1, \tau_2; \nu) = r(\nu)|A(\tau_1, \tau_2)| - a(\nu, \tau_1)S_1(\tau_2; \tau_1) - a(\nu, \tau_2)S_1(\tau_1; \tau_2)$. Differentiating with respect to $\tau_2$ yields that

$$\partial_{0,1,0}S_2(\tau_1, \tau_2; \nu) \;=\; r(\nu)\partial_{0,1}|A(\tau_1, \tau_2)| - a(\nu, \tau_1)\partial_{1,0}S_1(\tau_2; \tau_1) - \partial_{0,1}a(\nu, \tau_2)S_1(\tau_1.\tau_2) - a(\nu, \tau_2)\partial_{0,1}S_1(\tau_1; \tau_2).$$

By taking $\tau_2$ equal to $\tau_1$, and using that $\partial_{0,1}|A(\tau_1, \tau_1)| = 0$ (Lemma 9.1) and $S_1(\tau_1; \tau_1) = 0$ we obtain that $\partial_{0,1,0}S_2(\tau_1, \tau_1; \nu) = -a(\nu, \tau_1)(\partial_{1,0}S_1(\tau_1; \tau_1) + \partial_{0,1}S_1(\tau_1; \tau_1)) = 0$, since the function $\tau \mapsto S_1(\tau; \tau)$ is equal to the zero function.

The induction hypothesis states that $\partial_{0,\ldots,0,1,0}S_{k-1}(\tau_1, \ldots, \tau_{k-2}, \tau_{k-2}; \nu) = 0$. Writing (again by (5.47)) $S_k(\tau_1, \ldots, \tau_k; \nu) = r(\nu)|A(\tau_1, \ldots, \tau_k)| - \sum_{i=1}^{k} a(\nu, \tau_i)S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i)$ and differentiating with respect to $\tau_k$ we get that

$$\begin{aligned}
\partial_{0,\ldots,0,1,0}S_k(\tau_1, \ldots, \tau_k; \nu) \;&=\; \\
r(\nu)\partial_{0,\ldots,0,1}|A(\tau_1, \ldots, \tau_k)| \;&-\; \sum_{i=1}^{k-2} a(\nu, \tau_i)\partial_{0,\ldots,0,1,0}S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i) - a(\nu, \tau_{k-1})\partial_{0,\ldots,0,1,0}S_{k-1}(\tau_1, \ldots, \tau_{k-2}, \tau_k; \tau_{k-1}) - \\
&\partial_{0,1}a(\nu, \tau_k)S_{k-1}(\tau_1, \ldots, \tau_{k-1}; \tau_k) - a(\nu, \tau_k)\partial_{0,\ldots,0,1}S_{k-1}(\tau_1, \ldots, \tau_{k-1}; \tau_k). \qquad (5.78)
\end{aligned}$$

Taking $\tau_k = \tau_{k-1}$ sets $\partial_{0,\ldots,0,1}|A(\tau_1, \ldots, \tau_{k-1}, \tau_k)|$ equal to 0 (Lemma 9.1), as well as $\partial_{0,\ldots,0,1,0}S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_i; \tau_i)$ for $i = 1, \ldots, k-2$ (induction hypothesis) and $S_{k-1}(\tau_1, \ldots, \tau_{k-1}; \tau_k)$. The remaining part in the right hand side of (5.78) becomes

$-a(\nu,\tau_{k-1})(\partial_{0,\dots,0,1,0}S_{k-1}(\tau_1,\dots,\tau_{k-2},\tau_{k-1};\tau_{k-1})+\partial_{0,\dots,0,1}S_{k-1}(\tau_1,\dots.\tau_{k-1};\tau_{k-1}))$, which again equals 0 since $\tau\mapsto S_{k-1}(\tau_1,\dots,\tau_{k-2},\tau;\tau)$ is identical to the zero function.

### 5.5.5 *Proof of Lemma 11*

#### 5.5.5.1 *Proof of Lemma 11.1*

In (5.57) we take $l = 1$, and $j_1 = j \in \{1, \ldots, k\}$ and obtain the equality

$$|A(\tau_1, \ldots, \tau_k \setminus \tau_j)|\; S_k(\tau_1, \ldots, \tau_k; \tau_{k+1}) \;-\; |A(\tau_1, \ldots, \tau_k)|\; S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_{k+1}) \;=\; (-1)^{j-(k+1)} |A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|\; S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_j). \quad (5.79)$$

Differentiating with respect to $\tau_{k+1}$ we get that

$$|A(\tau_1, \ldots, \tau_k \setminus \tau_j)|\; \partial_{0,\ldots,0,1} S_k(\tau_1, \ldots, \tau_k; \tau_{k+1}) \;-\; |A(\tau_1, \ldots, \tau_k)|\; \partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_{k+1}) \;=\; (-1)^{j-(k+1)} \partial_{0,\ldots,0,1} |A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|\; S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_j). \quad (5.80)$$

Setting $\tau_{k+1} = \tau_k$, and using the fact that $\langle \tau_1, \ldots, \tau_k \rangle \in \mathbb{A}_k$ belongs to the $k$-isocline yields that

$$-\,|A(\tau_1, \ldots, \tau_k)|\; \partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_k) \;=\; (-1)^{j-(k+1)} \frac{d|A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_j), \quad (5.81)$$

i.e.,

$$\partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_k) \;=\; (-1)^{j-(k+1)} \frac{d|A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k} \hat{x}_j(\tau_1, \ldots, \tau_k). \quad (5.82)$$

Since $\hat{x}_j(\tau_1, \ldots, \tau_k) > 0$, it follows that

$$\operatorname{sign}\big(\partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_k)\big) \;=\; -\operatorname{sign}\Big((-1)^{j-k} \frac{d|A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k}\Big). \quad (5.83)$$

### 5.5.5.2 *Proof of Lemma 11.2*

In (5.56) we replace $k$ by $k+1$, take $l=1$ and $j_1 = j \in \{1,\dots,k-1\}$, and $i=k+1$. We obtain the equality

$$|A(\tau_1,\dots,\tau_{k+1}\setminus\tau_j)|\ S_k(\tau_1,\dots,\tau_k;\tau_{k+1}) \ - \ |A(\tau_1,\dots,\tau_{k+1})|\ S_{k-1}(\tau_1,\dots,\tau_k\setminus\tau_j;\tau_{k+1}) \ = \\ (-1)^{j-(k+1)}|A(\tau_1,\dots,\tau_{k+1})_{(j,k+1)}|\ S_k(\tau_1,\dots,\tau_{k+1}\setminus\tau_j;\tau_j). \quad (5.84)$$

Differentiating with respect to $\tau_{k+1}$ yields that

$$\partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_{k+1}\setminus\tau_j)|\ S_k(\tau_1,\dots,\tau_k;\tau_{k+1}) \ + \ |A(\tau_1,\dots,\tau_{k+1}\setminus\tau_j)|\ \partial_{0,\dots,0,1}S_k(\tau_1,\dots,\tau_k;\tau_{k+1}) \ - \\ \partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_k,\tau_{k+1})|\ S_{k-1}(\tau_1,\dots,\tau_k\setminus\tau_j;\tau_{k+1}) \ - \ |A(\tau_1,\dots,\tau_{k+1})|\ \partial_{0,\dots,0,1}S_{k-1}(\tau_1,\dots,\tau_k\setminus\tau_j;\tau_{k+1}) \ = \\ (-1)^{j-(k+1)}\partial_{0,\dots,0,1}|A(\tau_1,\dots,\tau_{k+1})_{(j,k+1)}|\ S_k(\tau_1,\dots,\tau_{k+1}\setminus\tau_j;\tau_j) \ + \\ (-1)^{j-(k+1)}|A(\tau_1,\dots,\tau_{k+1})_{(j,k+1)}|\ \partial_{0,\dots,0,1,0}S_k(\tau_1,\dots,\tau_{k+1}\setminus\tau_j;\tau_j). \quad (5.85)$$

Taking $\tau_{k+1}=\tau_k$ in this expression yields $0=0$. Differentiating twice with respect to $\tau_{k+1}$ in (5.84) renders the equality

$$\begin{multline}\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\;S_k(\tau_1,\ldots,\tau_k;\tau_{k+1})\;+\;2\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\;\partial_{0,\ldots,0,1}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1})\;+\\
|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\;\partial_{0,\ldots,0,2}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1})\;-\;\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\;S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1})\;-\\
2\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\;\partial_{0,\ldots,0,1}S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1})\;-\;|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\;\partial_{0,\ldots,0,2}S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1})\;=\\
(-1)^{j-(k+1)}\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\;S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j)\;+\\
(-1)^{j-(k+1)}\;2\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\;\partial_{0,\ldots,0,1,0}S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j)\;+\\
(-1)^{j-(k+1)}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\;\partial_{0,\ldots,0,2,0}S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j).\tag{5.86}\end{multline}$$

Taking $\tau_{k+1}$ equal to $\tau_k$, and making use of Corollary 6.5, Lemmas 9.1 and 10 yields again $0 = 0$. We differentiate once more with respect to $\tau_{k+1}$, and obtain

$$\begin{aligned}
&\partial_{0,\ldots,0,3}|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\; S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;+\; 3\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\; \partial_{0,\ldots,0,1}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;+\\
&3\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\; \partial_{0,\ldots,0,2}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;+\; |A(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j)|\; \partial_{0,\ldots,0,3}S_k(\tau_1,\ldots,\tau_k;\tau_{k+1}) \;-\\
&\partial_{0,\ldots,0,3}|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\; S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1}) \;-\; 3\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\; \partial_{0,\ldots,0,1}S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1}) \;-\\
&3\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\; \partial_{0,\ldots,0,2}S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1}) \;-\; |A(\tau_1,\ldots,\tau_k,\tau_{k+1})|\; \partial_{0,\ldots,0,3}S_{k-1}(\tau_1,\ldots,\tau_k\setminus\tau_j;\tau_{k+1}) \;=\\
&(-1)^{j-(k+1)}\partial_{0,\ldots,0,3}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\; S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j) \;+\\
&(-1)^{j-(k+1)}\; 3\partial_{0,\ldots,0,2}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\; \partial_{0,\ldots,0,1,0}S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j) \;+\\
&(-1)^{j-(k+1)}\; 3\partial_{0,\ldots,0,1}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\; \partial_{0,\ldots,0,2,0}S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j) \;+\\
&(-1)^{j-(k+1)}|A(\tau_1,\ldots,\tau_{k+1})_{(j,k+1)}|\; \partial_{0,\ldots,0,3,0}S_k(\tau_1,\ldots,\tau_{k+1}\setminus\tau_j;\tau_j).
\end{aligned} \tag{5.87}$$

We again take $\tau_{k+1} = \tau_k$. Using the fact that $\langle \tau_1, \ldots, \tau_k \rangle \in \mathbb{A}_k$ belongs to the $k$-isocline, as well as Corollary 6.5 and Lemmas 9.1 and 10, reduces the previous equality to

$$\partial_{0,\ldots,0,2} |A(\tau_1, \ldots, \tau_k, \tau_k)|\, \partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_k) \;= \qquad\qquad (-1)^{j-k} \frac{d|A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\bigg|_{\tau_{k+1}=\tau_k} \partial_{0,\ldots,0,2,0} S_k(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_j). \tag{5.88}$$

In the first part of the Lemma we derived that $\operatorname{sign}\big(\partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_k)\big) \;= -\operatorname{sign}\Big((-1)^{j-k} \frac{d|A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k}\Big)$. Since by assumption $\partial_{0,\ldots,0,2} s_k(\tau_1, \ldots, \tau_k; \tau_k) + \partial_{0,\ldots,0,2,0} s_k(\tau_1, \ldots, \tau_{k-1}, \tau_k; \tau_k) > 0$, we know from Lemma 9.2 and its proof that $\partial_{0,\ldots,0,2} |A(\tau_1, \ldots, \tau_k, \tau_k)| \neq 0$ (see (5.77)). We conclude from (5.88) that

$$\frac{\partial_{0,\ldots,0,2,0} S_k(\tau_1, \ldots, \tau_k, \tau_k \setminus \tau_j; \tau_j)}{\partial_{0,\ldots,0,2} |A(\tau_1, \ldots, \tau_k, \tau_k)|} = (-1)^{j-k} \frac{\partial_{0,\ldots,0,1} S_{k-1}(\tau_1, \ldots, \tau_k \setminus \tau_j; \tau_k)}{\frac{d|A(\tau_1, \ldots, \tau_{k+1})_{(j,k+1)}|}{d\tau_{k+1}}\Big|_{\tau_{k+1}=\tau_k}} < 0. \tag{5.89}$$

### 5.5.6 *Proof of Lemma 12*

Firstly, given that $LV_k(\tau_1,\ldots,\tau_k)$ is fully subregular, the fact that $LV_k(\tau'_1,\ldots,\tau'_k)$ is fully subregular for $(\tau'_1,\ldots,\tau'_k)$ sufficiently close to $(\tau_1,\ldots,\tau_k)$ follows immediately from the continuity of the function $(\tau_1,\ldots,\tau_k\setminus\tau_{i_1},\ldots,\tau_{i_l})\mapsto |A(\tau_1,\ldots,\tau_k\setminus\tau_{i_1},\ldots,\tau_{i_l})|$, for any $l=1.\ldots,k$ and any set $\{i_1,\ldots,i_l\}\subset\{1,\ldots,k\}$.

It remains to be shown that $s$-permanence of $LV_k(\tau_1,\ldots,\tau_k)$ is maintained under sufficiently small changes of $(\tau_1,\ldots,\tau_k)$ into $(\tau'_1,\ldots,\tau'_k)$. Let $p_1,\ldots,p_k$ be positive numbers such that for each $l=1,\ldots,k$ and each subset $\{i_1,\ldots,i_l\}\subset\{1,\ldots,k\}$ (with mutually distinct $i_1,\ldots,i_l$) for which $\hat{x}(\tau_1,\ldots,\tau_k\setminus\tau_{i_1},\ldots,\tau_{i_l})\in\operatorname{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists, the condition

$$\sum_{\alpha=1}^{l} p_{i_\alpha} s_{k-l}(\tau_1,\ldots,\tau_k\setminus\tau_{i_1},\ldots,\tau_{i_l};\tau_{i_\alpha})>0 \tag{5.90}$$

holds. We seek positive numbers $p'_1,\ldots,p'_k$ such that for each $l=1,\ldots,k$ and each subset $\{i_1,\ldots,i_l\}\subset\{1,\ldots,k\}$ (with $i_1,\ldots,i_l$ again mutually distinct) for which $\hat{x}(\tau'_1,\ldots,\tau'_k\setminus\tau'_{i_1},\ldots,\tau'_{i_l})\in\operatorname{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists,

$$\sum_{\beta=1}^{l} p'_{j_\beta} s_{k-l}(\tau'_1,\ldots,\tau'_k\setminus\tau'_{i_1},\ldots,\tau'_{i_l};\tau'_{i_\beta})>0. \tag{5.91}$$

We consider the generic and the non-generic case.

> Case I (The generic case.) For each $l=1,\ldots,k$ and each $\{i_1,\ldots,i_l\}\subset\{1,\ldots,k\}$, $\hat{x}(\tau'_1,\ldots,\tau'_k\setminus\tau'_{i_1},\ldots,\tau'_{i_l})\in\operatorname{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists if and only if $\hat{x}(\tau_1,\ldots,\tau_k\setminus\tau_{i_1},\ldots,\tau_{i_l})\in\operatorname{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists. The change from $(\tau_1,\ldots,\tau_k)$ into $(\tau'_1,\ldots,\tau'_k)$ then causes a change in the equilibrium values, but does not cause the appearance of additional equilibria. The positivity of the numbers $p_1,\ldots,p_k$, the continuity of the functions $(\tau_1,\ldots,\tau_k)\mapsto s_{k-l}(\tau_1,\ldots,\tau_k\setminus\tau_{i_1},\ldots,\tau_{i_l};\tau_{i_\alpha})$, $\alpha\in\{1,\ldots,l\}$, and the positivity of the summation in (5.90) then imply that there is an open neighbourhood $U$ of $(\tau_1,\ldots,\tau_k)$ in $\mathbb{T}^k$, and an open neighbourhood $V$ of $(p_1,\ldots,p_k)$ in $\operatorname{int}(\mathbb{R}^k_+)$, such that for any $(\tau'_1,\ldots,\tau'_k)\in U$ and any $(p'_1,\ldots,p'_k)\in V$ expression (5.91) is satisfied for each $l=1,\ldots,k$ and each subset $\{i_1,\ldots,i_l\}\subset\{1,\ldots,k\}$ for which $\hat{x}(\tau'_1,\ldots,\tau'_k\setminus\tau'_{i_1},\ldots,\tau'_{i_l})\in\operatorname{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists.

Case II (The non-generic case.) Let $I$ denote the collection of sets $\{i_1,\ldots,i_l\} \subset \{1,\ldots,k\}$ (for any $l = 1,\ldots,k$) for which $\hat{x}(\tau_1,\ldots,\tau_k \setminus \tau_{i_1},\ldots,\tau_{i_l}) \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists. Under sufficiently small changes of $(\tau_1,\ldots,\tau_k)$ into $(\tau_1',\ldots,\tau_k')$, then also the equilibrium $\hat{x}(\tau_1',\ldots,\tau_k' \setminus \tau_{i_1}',\ldots,\tau_{i_l}') \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists. In the non-generic case in addition there is a sub-collection $J$ of these sets $\{i_1,\ldots,i_l\}$ such that for each element in $J$ there exists at least one non-empty subset $\{j_1,\ldots,j_{l'}\} \subset \{i_1,\ldots,i_l\}$, with $l' < l$, for which the equilibrium $\hat{x}(\tau_1',\ldots,\tau_k' \setminus \tau_{j_1}',\ldots,\tau_{j_{l'}}') \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+))$ comes into existence due to the change from $(\tau_1,\ldots,\tau_k)$ into $(\tau_1',\ldots,\tau_k')$ (which implies that $\{j_1,\ldots,j_{l'}\}$ itself does not belong to $I$). For a given $\{i_1,\ldots,i_l\} \in J$ and $\{j_1,\ldots,j_{l'}\} \subset \{i_1,\ldots,i_l\}$ this happens if due to this change a bifurcation occurs in which $\hat{x}(\tau_1,\ldots,\tau_k \setminus \tau_{i_1},\ldots,\tau_{i_l}) \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ splits into two equilibria: $\hat{x}(\tau_1',\ldots,\tau_k' \setminus \tau_{i_1}',\ldots,\tau_{i_l}') \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ and $\hat{x}(\tau_1',\ldots,\tau_k' \setminus \tau_{j_1}',\ldots,\tau_{j_{l'}}') \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+))$. For $LV_k(\tau_1,\ldots,\tau_k)$ it then is required that, with $\alpha \in \{1,\ldots,k\} \setminus \{i_1,\ldots,i_l\}$ and $\beta \in \{i_1,\ldots,i_l\} \setminus \{j_1,\ldots,j_{l'}\}$, the restriction to $\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+)$ of the isoclines $r(\tau_\alpha) + \sum_{j=1}^{k} a(\tau_\alpha,\tau_j)x_j = 0$ and $r(\tau_\beta) + \sum_{j=1}^{k} a(\tau_\beta,\tau_j)x_j = 0$ (i.e., $r(\tau_\alpha) + \sum_{\substack{j=1 \\ j\notin\{j_1,\ldots,j_{l'}\}}}^{k} a(\tau_\alpha,\tau_j)x_j = 0$ and $r(\tau_\beta) + \sum_{\substack{j=1 \\ j\notin\{j_1,\ldots,j_{l'}\}}}^{k} a(\tau_\beta,\tau_j)x_j = 0$) intersect in $\hat{x}(\tau_1,\ldots,\tau_k \setminus \tau_{i_1},\ldots,\tau_{i_l}) \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$. Consequently,

$$s_{k-l}(\tau_1,\ldots,\tau_k \setminus \tau_{i_1},\ldots,\tau_{i_l};\tau_\beta) = 0 \quad \text{for } \beta \in \{i_1,\ldots,i_l\} \setminus \{j_1,\ldots,j_{l'}\}. \tag{5.92}$$

In the community state space of $LV_k(\tau_1',\ldots,\tau_k')$ the equilibrium $\hat{x}(\tau_1',\ldots,\tau_k' \setminus \tau_{i_1}',\ldots,\tau_{i_l}') \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ then is the intersection of the restriction to $\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+)$ of the isoclines $r(\tau_\alpha') + \sum_{j=1}^{k} a(\tau_\alpha',\tau_j')x_j = 0$, $\alpha \in \{1,\ldots,k\} \setminus \{i_1,\ldots,i_l\}$, with $\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+)$. The equilibrium $\hat{x}(\tau_1',\ldots,\tau_k' \setminus \tau_{j_1}',\ldots,\tau_{j_{l'}}') \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+))$ is the intersection of the isoclines $r(\tau_\alpha') + \sum_{j=1}^{k} a(\tau_\alpha',\tau_j')x_j = 0$, $\alpha \in \{1,\ldots,k\} \setminus \{i_1,\ldots,i_l\}$, with the isoclines

$r(\tau'_\beta) + \sum_{j=1}^{k} a(\tau'_\beta, \tau'_j)x_j$, $\beta \in \{i_1, \ldots, i_l\} \setminus \{j_1, \ldots, j_{l'}\}$, with both collections of isoclines restricted to $\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+)$.

As in the generic case, it follows that there exist a neighbourhood $U_1$ of $(\tau'_1, \ldots, \tau'_k)$ in $\mathbb{T}^k$ and a neighbourhood $V_1$ of $(p'_1, \ldots, p'_k)$ in $\mathrm{int}(\mathbb{R}^k_+)$ such that (5.91) is satisfied for all $(\tau'_1, \ldots, \tau'_k) \in U_1$ and all $(p'_1, \ldots, p'_k) \in V_1$, for all equilibria $\hat{x}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{i_1}, \ldots, \tau'_{i_l}) \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$, for all $l = 1, \ldots, k$ and all $\{i_1, \ldots, i_l\} \in I \setminus J$.

Next, let $\{i_1, \ldots, i_l\} \in J$, and $\{j_1, \ldots, j_{l'}\} \subset \{i_1, \ldots, i_l\}$, such that under the change from $(\tau_1, \ldots, \tau_k)$ into $(\tau'_1, \ldots, \tau'_k)$ the equilibrium $\hat{x}(\tau_1, \ldots, \tau_k \setminus \tau_{i_1}, \ldots, \tau_{i_l}) \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ splits into $\hat{x}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{i_1}, \ldots, \tau'_{i_l}) \in \mathrm{int}(\mathrm{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ and $\hat{x}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{j_1}, \ldots, \tau'_{j_{l'}}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l'}}(\mathbb{R}^k_+))$. For any such set $\{i_1, \ldots, i_l\} \in J$ expression (5.90) due to (5.92) can be rewritten as

$$\sum_{\substack{\alpha=1 \\ i_\alpha \in \{j_1,\ldots,j_{l'}\}}}^{l} p_{i_\alpha} s_{k-l}(\tau_1, \ldots, \tau_k \setminus \tau_{i_1}, \ldots, \tau_{i_l}; \tau_{i_\alpha}) > 0. \tag{5.93}$$

For $\hat{x}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{i_1}, \ldots, \tau'_{i_l})$ it follows (for any numbers $p'_1, \ldots, p'_k$) that

$$\begin{aligned}\sum_{\alpha=1}^{l} p'_{i_\alpha} s_{k-l}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{i_1}, \ldots, \tau'_{i_l}; \tau'_{i_\alpha}) &= \\ &\sum_{\substack{\alpha=1 \\ i_\alpha \in \{j_1,\ldots,j_{l'}\}}}^{l} p'_{i_\alpha} s_{k-l}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{i_1}, \ldots, \tau'_{i_l}; \tau'_{i_\alpha}) + \\ &\sum_{\substack{\alpha=1 \\ i_\alpha \in \{i_1,\ldots,i_l\} \setminus \{j_1,\ldots,j_{l'}\}}}^{l} p'_{i_\alpha} s_{k-l}(\tau'_1, \ldots, \tau'_k \setminus \tau'_{i_1}, \ldots, \tau'_{i_l}; \tau'_{i_\alpha}).\end{aligned} \tag{5.94}$$

From (5.93) it follows for $(\tau'_1, \ldots, \tau'_k)$ sufficiently close to $(\tau_1, \ldots, \tau_k)$ and $(p'_1, \ldots, p'_k)$ sufficiently close to $(p_1, \ldots, p_k)$, that the first summation in the right hand side of this expression is positive, for any $\{i_1, \ldots, i_l\} \in J$. From (5.92) it follows that for $(\tau'_1, \ldots, \tau'_k)$ sufficiently close to $(\tau_1, \ldots, \tau_k)$ and $(p'_1, \ldots, p'_k)$ sufficiently close to $(p_1, \ldots, p_k)$, the second summation in (5.94) can be taken to be arbitrarily small, for any $\{i_1, \ldots, i_l\} \in J$. Therefore, there exist an open neighbourhood $U_2$ of $(\tau'_1, \ldots, \tau'_k)$ in $\mathbb{T}^k$ and an open neighbourhood $V_2$ of $(p_1, \ldots, p_k)$ in $\mathrm{int}(\mathbb{R}^k_+)$ such that (5.91) is satisfied for all $(\tau_1', \dots, \tau_k') \in U_2$ and all $(p_1', \dots, p_k') \in V_2$, for all equilibria $\hat{x}(\tau_1', \dots, \tau_k' \setminus \tau_{i_1}', \dots, \tau_{i_l}') \in \operatorname{int}(\mathrm{bd}_{i_1,\dots,i_l}(\mathbb{R}_+^k))$, for all $l = 1, \dots, k$ and all $\{i_1, \dots, i_l\} \in J$.

For $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\} \in J$ we notice, by Lemma 4 and expression (5.92), that $s_{k-l'}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l'}}; \tau_{j_\beta})$ equals $s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{j_\beta})$, $\beta = 1, \dots, l'$. Therefore, with (5.93),

$$\sum_{\beta=1}^{l'} p_\beta s_{k-l'}(\tau_1, \dots, \tau_k \setminus \tau_{j_1}, \dots, \tau_{j_{l'}}; \tau_{j_\beta}) = \sum_{\beta=1}^{l'} p_\beta s_{k-l}(\tau_1, \dots, \tau_k \setminus \tau_{i_1}, \dots, \tau_{i_l}; \tau_{j_\beta}) > 0. \quad (5.95)$$

It follows that there exist an open neighbourhood $U_3$ of $(\tau_1, \dots, \tau_k)$ in $\mathbb{T}^k$ and an open neighbourhood $V_3$ of $(p_1, \dots, p_k)$ in $\operatorname{int}(\mathbb{R}_+^k)$ such that (5.91) is satisfied for all $(\tau_1', \dots, \tau_k') \in U_3$ and all $(p_1', \dots, p_k') \in V_3$, for all possible equilibria $\hat{x}(\tau_1', \dots, \tau_k' \setminus \tau_{j_1}', \dots, \tau_{j_{l'}}') \in \operatorname{int}(\mathrm{bd}_{j_1,\dots,j_{l'}}(\mathbb{R}_+^k))$, for all $l = 1, \dots, k$ and all $\{j_1, \dots, j_{l'}\} \subset \{i_1, \dots, i_l\} \in J$.

By taking $(\tau_1', \dots, \tau_k') \in U_1 \cap U_2 \cap U_3$ and $(p_1', \dots, p_k') \in V_1 \cap V_2 \cap V_3$ it follows that (5.91) holds for any $l = 1, \dots, k$ and any $\{i_1, \dots, i_l\} \subset \{1, \dots, k\}$ for which the equilibrium $\hat{x}(\tau_1', \dots, \tau_k' \setminus \tau_{i_1}, \dots, \tau_{i_l}) \in \operatorname{int}(\mathrm{bd}_{i_1,\dots,i_l}(\mathbb{R}_+^k))$ exists. This proves the non-generic case.

### 5.5.7 *Proof of Lemma 13*

Without loss of generality we may assume that $i$ equals $k$, and we shall do so here.

The $s$-permanence of $LV_k(\tau_1, \ldots, \tau_k)$ implies the existence of $k$ strictly positive numbers $p_1, \ldots, p_k$ such that for each $l$ and each subset $\{i_1, \ldots, i_l\} \subset \{1, \ldots, k\}$ such that $\hat{x}(\tau_1, \ldots, \tau_k \setminus \tau_{i_1}, \ldots, \tau_{i_l}) \in \operatorname{int}(\operatorname{bd}_{i_1,\ldots,i_l}(\mathbb{R}^k_+))$ exists,

$$\sum_{\alpha=1}^{l} p_{i_\alpha} s_{k-l}(\tau_1, \ldots, \tau_k \setminus \tau_{i_1}, \ldots, \tau_{i_l}; \tau_{i_\alpha}) > 0. \tag{5.96}$$

We seek $k+1$ strictly positive numbers $p'_1, \ldots, p'_{k+1}$ such that for each $l = 1, \ldots, k+1$ and each subset $\{j_1, \ldots, j_l\} \subset \{1, \ldots, k+1\}$ (of mutually distinct elements) for which $\hat{x}(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_l}) \in \operatorname{int}(\operatorname{bd}_{j_1,\ldots,j_l}(\mathbb{R}^{k+1}_+))$ exists, the summation

$$\sum_{\beta=1}^{l} p'_{j_\beta} s_{k+1-l}(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_l}; \tau_{j_\beta}). \tag{5.97}$$

is positive.

We first restrict ourselves to the case $l = 1$. For each $j \in \{1, \ldots, k+1\}$ such that $\hat{x}(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_j) \in \operatorname{int}(\operatorname{bd}_j(\mathbb{R}^{k+1}_+))$ exists, $p'_j s_k(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j) > 0$ then is required to hold. I.e., both

$$p'_k s_k(\tau_1, \ldots, \tau_{k-1}, \tau_{k+1}; \tau_k) > 0, \tag{5.98}$$

and

$$p'_{k+1} s_k(\tau_1, \ldots, \tau_k; \tau_{k+1}) > 0 \tag{5.99}$$

must hold, and in addition for each $j = 1, \ldots, k-1$

$$p'_j s_k(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j) > 0 \tag{5.100}$$

must hold. Since both $s_k(\tau_1, \ldots, \tau_{k-1}, \tau_{k+1}; \tau_k) > 0$ and $s_k(\tau_1, \ldots, \tau_k; \tau_{k+1}) > 0$ for $\tau_{k+1}$ sufficiently close (but not equal) to $\tau_k$, it follows that in case $l = 1$, $p'_k$ and $p'_{k+1}$ can taken to be arbitrarily positive numbers. For $j = 1, \ldots, k-1$, we obtain from (5.66) that for $\tau_{k+1}$ sufficiently close (but not equal) to $\tau_k$ that $\hat{x}_j(\tau_1, \ldots, \tau_{k+1}) > 0$. With (5.49) and Lemma 9.2 it then follows for such $\tau_{k+1}$ that $s_k(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_j; \tau_j) > 0$. This then implies that for $l = 1$ also the $p'_j$, $j = 1, \ldots, k-1$, in (5.100) can taken to be arbitrarily positive numbers. We conclude that there is an open neighbourhood $U_1$ of $\tau_k$ in $\mathbb{R}$ such that for each $\tau_{k+1} \neq \tau_k$ in $U_1$, expression (5.97) is positive for $l = 1$ and each $j \in \{1, \ldots, k+1\}$ such that $\hat{x}(\tau_1, \ldots, \tau_{k+1} \setminus \tau_j) \in \text{int}(\text{bd}_j(\mathbb{R}^{k+1}_+))$ exists, for arbitrarily positive $p'_1 \ldots, p'_{k+1}$

We now consider $l = 2, \ldots, k+1$. We distinguish four mutually exclusive cases for the summations (5.97), that together cover all possible summations as determined by the sets $\{j_1, \ldots, j_l\} \subset \{1, \ldots, k+1\}$, $l = 2, \ldots, k+1$. We assume the $j_\beta$, $\beta = 1, \ldots, l$ to satisfy $j_1 < \cdots < j_l$.

1. $j_{l-1} = k, j_l = k+1$. The summation (5.97) then becomes

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; + \; p'_{k+1} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{k+1}) \; =$$

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; + \; p'_{k+1} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_k) \; +$$

$$\epsilon p'_{k+1} \partial_{0,\ldots,0,1} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_k) \; + \; o(\epsilon^2) \;\; (\epsilon \to 0). \quad (5.101)$$

By taking $p'_{j_\beta}$ to be equal to $p_{j_\beta}$, for $\beta = 1, \ldots, l-1$, the first summation in the last expression by assumption becomes positive, for each choice of $l \in \{2, \ldots, k+1\}$ and each $\{j_1, \ldots, j_{l-2}\} \subset \{1, \ldots, k-1\}$ such that $\hat{x}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l-1}}(\mathbb{R}^k_+))$ exists. By taking $p'_{k+1}$ positive and such that

$$p'_{k+1} < \min_{\substack{l=2,\ldots,k+1 \\ \{j_1,\ldots,j_{l-2}\}\subset\{1,\ldots,k-1\} \\ \hat{x}(\tau_1,\ldots,\tau_k\setminus\tau_{j_1},\ldots,\tau_{j_{l-1}})\in int(\mathrm{b}d_{j_1,\ldots,j_{l-1}}(\mathbb{R}^k_+))}} \frac{\sum_{\beta=1}^{l-1} p_{j_\beta} s_{k-(l+1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta})}{|s_{k-(l+1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_k)|}, \tag{5.102}$$

it follows that for $\tau_{k+1} \neq \tau_k$ sufficiently close to $\tau_k$, expression (5.97) then is positive. I.e., there is an open neighbourhood $U_2$ of $\tau_k$ in $\mathbb{R}$ such that for each $\tau_{k+1} \neq \tau_k$ that belongs to $U_2$, expression (5.97) is positive for $l = 2, \ldots, k+1$ and $\{j_1, \ldots, j_l\} \subset \{1, \ldots, k+1\}$, with $j_l = k$, $j_{l+1} = k+1$, and such that $\hat{x}(\tau_1, \ldots, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_l}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_l}(\mathbb{R}^{k+1}_+))$ exists.

2. $k \notin \{j_1, \ldots, j_{l-1}\}, j_l = k+1$. We then obtain that (5.97) equals

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; + \; p'_{k+1} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{k+1}) \; =$$

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; + \; \epsilon p'_{k+1} \partial_{0,\ldots,0,1} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_k) \; + \; o(\epsilon^2) \;\; (\epsilon \to 0). \tag{5.103}$$

The first summation in the right hand side by assumption becomes positive by replacing $p'_{j_\beta}$ with $p_{j_\beta}$, $\beta = 1, \ldots, l-1$, for each $l = 2, \ldots, k+1$ and each $\{j_1, \ldots, j_{1-1}\} \subset \{1, \ldots, k\}$ such that $\hat{x}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l-1}}(\mathbb{R}^k_+))$

exists. Consequently, there is an open neighbourhood $U_3$ of $\tau_k$ in $\mathbb{R}$ such that for each $\tau_{k+1} \neq \tau_k$ that belongs to $U_3$, expression (5.97) is positive for $l = 2, \ldots, k+1$ and $\{j_1, \ldots, j_l\} \subset \{1, \ldots, k+1\}$, with $k \notin \{j_1, \ldots, j_{l-1}\}$ and $j_l = k+1$, and such that $\hat{x}(\tau_1, \ldots, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_l}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_l}(\mathbb{R}^{k+1}_+))$ exists.

3. $j_l = k$ (and, consequently, $k+1 \notin \{j_1, \ldots, j_l\}$). The summation in (5.97) then yields

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \ldots, \tau_{k-1}, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; + \; p'_k s_{k-(l-1)}(\tau_1, \ldots, \tau_{k-1}, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_k) \; =$$

$$\sum_{\beta=1}^{l-1} p'_{j_\beta} s_{k-(l-1)}(\tau_1, \ldots, \tau_{k-1}, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; + \; \epsilon \sum_{\beta=1}^{l-1} p'_{j_\beta} \partial_{0,\ldots,0,1,0} s_{k-(l-1)}(\tau_1, \ldots, \tau_{k-1}, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_{j_\beta}) \; +$$

$$\epsilon p'_k \partial_{0,\ldots,0,1,0} s_{k-(l-1)}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}; \tau_k) \; + \; o(\epsilon^2) \;\; (\epsilon \to 0). \quad (5.104)$$

In the right hand side of (5.104), the first summation by assumption becomes positive by replacing $p'_{j_\beta}$ by $p_{j_\beta}$, $\beta = 1, \ldots, l-1$, for each $l = 2, \ldots, k+1$ and each $\{j_1, \ldots, j_{l-1}\} \subset \{1, \ldots, k-1\}$ such that $\hat{x}(\tau_1, \ldots, \tau_k \setminus \tau_{j_1}, \ldots, \tau_{j_{l-1}}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_{l-1}}(\mathbb{R}^k_+))$ exists. It follows that here is a neighbourhood $U_4$ of $\tau_k$ in $\mathbb{R}$ such that for each $\tau_{k+1} \neq \tau_k$ that belongs to $U_4$ expression (5.97) is positive for each $l = 2, \ldots, k+1$ and $\{j_1, \ldots, j_l\} \subset \{1, \ldots, k\}$, with $j_l = k$, and such that $\hat{x}(\tau_1, \ldots, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_l}) \in \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_l}(\mathbb{R}^{k+1}_+))$ exists.

4. Both $k \notin \{j_1, \ldots, j_l\}$ and $k+1 \notin \{j_1, \ldots, j_l\}$. This case does not have to be taken into account, since generically $\hat{x}(\tau_1, \ldots, \tau_k, \tau_{k+1} \setminus \tau_{j_1}, \ldots, \tau_{j_l}) \notin \mathrm{int}(\mathrm{bd}_{j_1,\ldots,j_l}(\mathbb{R}^{k+1}_+))$. This can be seen from expression (5.49). By this expression

$$\hat{x}_{\tau_k}(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l}) = -\frac{S_{k-l}(\tau_1,\ldots,\tau_{k-1},\tau_{k+1}\setminus,\tau_{j_1},\ldots,\tau_{j_l};\tau_k)}{|A(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l})|}, \text{ and}$$

$\hat{x}_{\tau_{k+1}}(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l}) = -\dfrac{S_{k-l}(\tau_1,\ldots,\tau_{k-1},\tau_k\setminus\tau_{j_1},\ldots,\tau_{j_l};\tau_{k+1})}{|A(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l})|}$. It follows that for $\tau_k$ and $\tau_{k+1}$ sufficiently close to each other, the values $\hat{x}_{\tau_k}(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l})$ and $\hat{x}_{\tau_{k+1}}(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l})$ have opposite signs, and therefore $\hat{x}(\tau_1,\ldots,\tau_k,\tau_{k+1}\setminus\tau_{j_1},\ldots,\tau_{j_l}) \notin \text{int}(\text{bd}_{j_1,\ldots,j_l}(\mathbb{R}^{k+1}_+))$.

We conclude that if $\tau_{k+1} \in U_1 \cap U_2 \cap U_3 \cap U_4$ and not equal to $\tau_k$, (5.97) is positive for all $l = 1,\ldots,k$ and all $\{j_1,\ldots,j_l\} \subset \{1,\ldots,k\}$ such that $\hat{x}(\tau_1,\ldots,\tau_{k+1}\setminus\tau_{j_1},\ldots,j_l) \in \text{bd}(\mathbb{R}^{k+1}_+)$, with the $p'_j$ equal to $p_j > 0$, $j = 1,\ldots,k$, and with $p'_{k+1} > 0$ satisfying expression (5.102). Therefore $LV_{k+1}(\tau_1,\ldots,\tau_{k+1})$ then is $s$-permanent.