適応ダイナミクスにおける侵入指数の数学的な基礎付けに関する研究

Mathematical foundation of invasion exponents associated with adaptive dynamics

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概要

本研究では、単性生殖する種の集団において、実数値をもつ量的表現型の形質値 (以下、省略して形質値) の進化を記述する適応ダイナミクスと呼ばれる数理モデルの数学的な基礎づけを目的とする。

大多数の個体が同一の形質値をもつ一つの種の集団において、集団で支配的な個体群 (residents) から mutation によって新たな形質値をもつ微小個体群 (mutants) が発生したとすると、residents と mutants の間で生存競争が発生する。mutation によって発生した生存競争において、一方の個体群が勝利して新たに集団の大多数を占めることにより集団の形質値が置換される。したがって “mutation から selection までの 1 サイクル” を、集団が持つ形質値の進化の 1 ステップとみなすことができる。適応ダイナミクスの大まかな枠組みは、この進化の 1 ステップを繰り返すことで集団の形質値が step-by-step に変動していく様子を調べることである。

しかしこのままでは mutation が発生するたびに、二つの個体群の間の競争を記述する力学系（競争モデル）を調べることになり、長期間に渡る進化の様子を解析する上では不便である。そこで、adapteive dyanmics の理論では、競争モデルにおいて “どちらの個体群が最終的に集団の大多数を占めるか” という情報を反映した “侵入指数” と呼ばれる量が抽出できるということを仮定する。そしてその侵入指数を用いた “pairwise invasilibity plots method” (省略して PIP 法) と呼ばれる手法で、進化の過程を解析するのである。このような “侵入指数” の抽出や、PIP 法の数学的な妥当性を検証することが、本論文の大きな目的である。

第 1 章第 1 節では侵入指数の定義と PIP 法のアルゴリズムを述べ、それらを用いてどのように進化の振る舞いを調べることができるかについて概説する。第 1 章第 2 節では、競争モデルから侵入指数の候補となる量を抽出する具体的な方法を述べる。また、抽出された “侵入指数の候補” が実際に侵入指数として正当化されている具体的なモデルのうち、本研究において重要なものを紹介する。

さて、適応ダイナミクス研究の大きな課題の一つは「与えられた個体群動態モデルから抽出された “侵入指数の候補” が侵入指数としての要件を満たす」という仮説が一般には未解決であったことである。この仮説に対して、

“invasion implies substitution principle” (省略して IIS principle) と呼ばれる原理の成否の研究が、適応度の母関数と呼ばれる関数が存在するという仮定の下で行われてきた。IIS principle は、突然変異で出現した個体群の出現時点における初期の局所的な振る舞いが、その個体群が大多数を占めるという状態の大域的な安定性を決定するというものである。それは数学的に言えば、力学系の固定点の局所的な安定性が力学系の大域的な振る舞いを決定するということになる。適応度の母関数が存在するという仮定の下で IIS principle が成立することは、Geritz、Dercole、Rinaldi らの先行研究によって明らかになっていた。

本研究ではまず、適応度の母関数の存在条件に対して簡単に検証可能な必要十分条件を与えた。さらに、この結果を用いて、異なる戦略をもつ 2 つの個体群の競争を記述するモデルの範疇においても、適応度の母関数の存在は、系の微小な摂動により崩壊することを示した。これは、すなわち「IIS principle の系の微小な摂動に関する安定性については、先行研究の結果からは得られない」ことを意味する。この問題に対して、本研究では、従来 IIS principle の研究で用いられていた invasion fitness の拡張として、raw invasion fitness という概念を導入することで、適応度の母関数が存在しない場合も含めた IIS principle が成立するための十分条件を示した。この結果によって、異なる戦略を持つ 2 つの個体群の種内競争を表すモデルの範疇において IIS principle の微小な摂動に対する安定性を示した。

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Introduction

Darwin's theory of evolution is one of the most stimulating fields of natural science to investigate the origin and the history of biological species. Results and methods in theoretical study of evolution have been contributing to investigation in biology as well as in other fields such as social science studying the mechanism how the human society has obtained indirect reciprocity.

In Darwinism, the process of biological evolution can be separated into three basic components: *replication*, *mutation* and *selection*. For simplicity we will consider asexual species. When a living organism reproduce, genetic information of the progenitor, called *genotype*, determined by base sequences of DNA or RNA, is usually inherited to its offspring. At each genetic replication, however, errors can occur in the process of copying the base sequences, and, as a result, a new organism having different genotype could emerges. Mutation in genotype causes diversity in genetic information, and moreover phenotypic traits (such as physical features and behaviors that can be inherited from generation to generation) could also be altered in association with the change of genotype. An individual that has different phenotype from its progenitor due to mutation is called *mutant*, and an individual that has one of the dominant strategies in the population is called *resident*. Because of the difference of phenotypic traits, mutants may have superiority or inferiority in struggle for existence to the progenitors in the population, that is often measured by the quality of *absolute fitness*, that is, the expected number of next generation born from a living organism. The difference of fitnesses among phenotypic trait values will finally result in *selection*. The three components, reproduction, mutation and selection, construct the basic mechanism of evolution.

Generally the correspondence between genotypes and phenotypes is neither of right nor of left univalent. Although numerous theoretical approaches to understand evolutionary phenomena have been proposed, it is difficult to describe the process of evolution of genotypic traits because of the lack of one-to-one correspondence. Whereas, a theoretical study of the correspondence of phenotypic trait values and their fitnesses, called *evolutionary game theory*, was introduced by Maynard Smith and Price in [25].

Consider a population, whose members play the role of players of a given matrix game, and each of them takes his/her own strategy. Maynard Smith and Price considered that the expected benefit of a strategy induced from a given matrix game equals to the fitness of the strategy. Their philosophy was mathematically formalized by Taylor and Jonker in [26] as a dynamical system of ODEs, called *replicator dynamics*, that describes selection in the population. See the definition of (1.2.2) in Section 1.2. Maynard Smith and Price introduced such notion of *evolutionarily stable strategy*, ESS for short, that, if all members of a population take an ESS, then no mutation is successful, that is, the group having newly emerged strategy by mutation will soon end up with extinction by selection. In other words, a population at an ESS is "stable" in regard to mutation, and ESSs work as fixed points of the process of evolution.

By the works by Eshel [11] and Nowak [21], however, it is found that ESSs are not always play the role of attracting points of the process of evolution and analyses of the course of evolution have become an intriguing topic in theoretical study of adaptive evolution. Simply speaking, adaptive evolution is a process of gradual change of dominant strategy in a population induced by the iteration of (MUT) and (COM):

(MUT) In a population having a dominant strategy (resident), mutation causes emergence of new strategy (mutant).

(COM) Selection makes one strategy go extinct and the other one become new dominant strategy of the population.

Geritz et al. [15] introduced a graphical method called *pairwise invasibility plots*, PIP for short, which helps to investigate step-by-step evolutionary processes, called *trait substitution sequence*, TSS for short. Consider a population that has two strategies x and y. Let us assume the existence of a real-valued function $\theta(x, y)$ whose structure determines which strategy will become a new dominant strategy in the population. Such function $\theta(x, y)$ is called *invasion exponent* and generally determined by either of absolute fitness or relative fitness. The PIP method determines the behavior of the process of evolution from the invasion exponent $\theta(x, y)$. To justify the PIP method, there are two processes:

1. To establish a model of evolution and extract the quantity $\theta(x, y)$ of "invasion exponent" from the model.

2. To show that the behavior of the evolution described by the model is determined by the “invasion exponent”.

Nowak [21] called such framework to analyze the process of evolution associated with a game *adaptive dynamics*, and Metz et al. [18] extended the scope of the theory to evolutionary processes associated with general population dynamics under density-dependent selection, adopting initial per-capita growth rate of mutant at the moment of mutation, called *invasion fitness*, as an invasion exponent of mutant strategy.

Let us assume that mutation event is rare enough, that is, mutation events never occur unless the competition due to the previous mutation is relaxed. Then one can completely separate the two timescales of the stochastic process (MUT) and the dynamical system (COM). The idea of adaptive dynamics is that, assuming mutational step to be small enough, one can justify PIP method associated with the invasion exponent obtained from the population dynamics of interest.

Following this philosophy, TSS can be constructed as a Markov jump process by iterating small and rare mutation and density-dependent selection. Taking a limit of TSS w.r.t. small mutational step size, one can derive a dynamical system of ODEs, called *canonical equation of adaptive dynamics*, CEAD for short, that is one of the main subjects of the field. The notion of CEAD was first proposed by Dieckmann and Law [9] and mathematically justified with the notion of TSS by Champagnat et al. [5]. In recent years, active research to deal with (MUT) and (COM) in one model has been carried out by describing reproduction, mutation and selection as a stochastic process, called *individual based model*, IBM for short. The study is motivated to derive TSS and CEAD from the same IBM, taking two limits w.r.t. large population size and small mutational step size at the same time. See Baar et al. [1] for example.

In this paper our main interest is the deterministic dynamical system of ODEs in (COM). More precisely, we are going to investigate how the outcome of the competition is determined, in other words, the global behavior of the dynamical system (COM). A typical scenario is that out of two equilibriums dominated by residents and mutants respectively, one of them is globally stable and the other is unstable.

Geritz et al. [14] have dealt with a discrete time model of a monomorphic[1] population having multiple attractors. In this model, there exists a

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[1] A population is said to be *k-morphic*, if there exists a set A of k-different strategies such that, for all $x \in A$, the population density of strategy x is positive. Especially, a population is respectively said to be *monomorphic*, *dimorphic* and *trimorphic* when k

pair of a resident dominant state and a mutant dominant state corresponding to each attractor of the monomorphic population. Making use of their own "tube theorem", which corresponds to a discrete version of Lemma A.1.2 in this paper, they have shown that if a shift between a resident dominant state and a mutant dominant state occurs, then those states constitute one of the pairs mentioned above corresponding to a single attractor of the monomorphic population. As for continuous time models, i.e. ODE models, Geritz [12] have gotten an analogue of the tube theorem for a special class of model, where he have shown the counterpart of the "invasion implies substitution" principle for his class. In fact, there exists a generating function for Geritz's model and hence the global stability can be determined by the invasion fitness.

In this direction, a remarkable achievements is the establishment of the *invasion-imply-substitution* principle, IIS principle for short, by Dercole and Rinaldi [8] under the assumption of the existence of generating function[4, 27], which includes Geritz's framework in [12]. The IIS principle is essentially equivalent to the claim that the "invasion fitness = invasion exponent" (denoted by $s_x(y)$ in [13, 10, 2]) ultimately determines which group survives, residents or mutants. See (2.1.6) for the definition. Mathematically, the invasion fitness is an index of the local stability of the resident-dominant equilibrium. Therefore, the IIS principle means that the local stability determines the global stability. In general, such an immediate coincidence of the local and the global stabilities is not at all obvious. There must be special feature in the system, which is the existence of generating function in the case of [8]. A natural question is what happens without such a strong constraint. One of our goals is to obtain a criterion of the global stability beyond IIS principle for a wider class which is still reasonable as a model of competition of residents and mutants. For this purpose, we are going to introduce the notion of raw invasion fitness Θ as a natural extension of invasion fitness and show the results including:

- Theorem 2.2.3: Uniform positivity (and negativity as well) of the local gradients of raw invasion fitness on the diagonal implies the shift of global stability between resident dominant state and mutant dominant state.
- Theorem 2.2.10: There exists a generating function associated with a dimorphic system if and only if the local gradients of raw invasion fitness on the diagonal only depends on the total population.

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equals to one, two and three. Find the precise definition in Section 1.1

Another reason to seek a theory beyond the existing IIS principle is the question on the stability of global behavior under perturbations of an original system. For example, let us consider the following system:

$$\begin{aligned} \frac{dn_1}{dt} &= n_1\big(1-(n_1+n_2)+(x_2-x_1)n_2(c-an_1-bn_2)\big) \\ \frac{dn_2}{dt} &= n_2\big(1-(n_1+n_2)+(x_1-x_2)n_1(c-an_2-bn_1)\big), \end{aligned} \tag{0.0.1}$$

where n_1 and n_2 are population densities of the groups having strategies x_1 and x_2 respectively. Note that if $a = b = 0$, then it has been known that IIS principle can be applied. If a and b are small, the above system can be thought of as a small perturbation of such a special case. On the other hand, Theorem 2.2.10 implies that there exists an associated generating function (and hence the existing IIS principle can be applied) if and only if $a = b$. Since a small perturbation to the system can easily destroy the equality $a = b$, we need a theory beyond the paradigm of invasion fitness in order to study the stability of the global behavior under small perturbations. Indeed, by our results, we do see that the global behavior of (0.0.1) is stable under small perturbations of the parameters a, b and c as long as $(b-c)(a+b-2c) \neq 0$. See Subsection 2.2.3 for details.

In the first chapter, we will introduce the basic notions of adaptive dynamics such as PIP method and invasion exponent. The derivation and justification of invasion exponents under two different types of selection will be also explained. The interest of this study is to justify the invasion exponent under density-dependent selection. We will describe our results in detail in the second chapter.

Chapter 1

The adaptive dynamics theory focusing on PIP method

As we have seen in Introduction, the gradual evolution of strategies i.e. phenotypic trait values is described as step-by-step alterations of dominant strategy induced by the iteration of stochastic model of mutation (MUT) and dynamical model of competition (COM). In the framework of adaptive dynamics, it has been assumed that one may extract, from the dynamical model (COM), a quantity called "invasion exponent" that is an indicator to know which group will win; residents or mutants. Thus the framework of adaptive dynamics is composed of the following four procedures.

1. To establish a dynamical model of competition between two groups; residents and mutants.
2. To extract a quantity, which is a candidate for invasion exponent, from the dynamical model of competition.
3. Based on the invasion exponent, to develop the theory to describe the process of evolution called *pairwise invasibility plots*, PIP for short.

Of course, one have to justify mathematically the legitimacy of the invasion exponent and the PIP method, which is actually one of the main purpose of this paper and discussed in the next chapter. For the time being in this chapter, we survey the existing theory of adaptive dynamics, i.e. several dynamical models of competition of residents and mutants, the extraction of invasion exponents from the dynamical models, and how the PIP method using the invasion exponent works. To empathize the role of invasion exponent, we are going to do our survey in the reversed order. Namely the first section of this chapter is devoted to explain what the invasion exponent is, what conditions an invasion exponent should satisfy (Principle of invasion exponents) and how to use an invasion exponent to predict the course of adaptive evolution (the PIP method). In the second section, we will actually extract invasion exponents from the two specific models and discuss about whether or not Principle of invasion exponents holds for them.

1.1 Pairwise invasivility plots: a graphical method for the analysis of evolutionary processes

In place of constructing a stochastic model of evolution, the graphical method called pairwise invasibility plots, PIP for short, has been widely used to investigate how the process of evolution behaves. For the use of the PIP method, we must not only extract a candidate for an invasion exponent from a given dynamical model of competition but also check whether the candidate satisfies the requirements for invasion exponent. First of all, we are going to introduce "Principle of invasion exponents" that provides the requirements for invasion exponent.

1.1.1 Principle of invasion exponensts

Consider a population of a biological species whose members reproduce their offsprings asexually. Let $X \subseteq \mathbb{R}$ be the collection of strategies i.e. phenotypic trait values. Let $n(t,x)$ be the population density of the group of individuals having the strategy x and let $N(t)$ be the total density of the population at time $t \geq 0$. We call a population *k-morphic* if

$$N(t) = \sum_{i=1}^{k} n(t, x_i),$$

for k-different strategies $x_1, \ldots, x_k \in X$. In particular population is said to be *monomorphic* and *dimorphic* when $k = 1$ and $k = 2$, respectively. For a finite subset $A \subset X$, we assume that the combination of population densities $(n(t,x))_{x \in A}$ is driven by a given dynamical model (COM). We call a population *A-dominant*, if

$$\liminf_{t \to \infty} n(t,x) > 0$$

for any $x \in A$. In particular $\{x\}$-dominant population is simply said to be x-dominant.

Consider an x-dominant population whose dynamics $(n(t,x))_{t\geq 0}$ driven by a dynamical system has already been relaxed to a stable equilibrium $\widehat{n}_x$, i.e.,

$$\lim_{t\to\infty} n(t,x) = \widehat{n}_x.$$

Now let a small mutation generate a new strategy $y \in X$ into the population, then the population dynamics $(n(t,x), n(t,y))_{t\geq 0}$ will be driven by another dynamical system (COM) with an initial state $(n(0,x), n(0,y))$ close to $(\widehat{n}_x, 0)$. What we need is an indicator that determines the result of this competition.

We assume the existence of a function $\theta : X \times X \to \mathbb{R}$ whose sign determines the course of the competition of two strategies in the following way;

Principle of invasion exponent

(A) *If* $\theta(x,y) < 0$, *mutants will disappear eventually and the population stays* x*-dominant, i.e.* $n(t,y) \to 0$.

(B) *If* $\theta(x,y) > 0$, *the mutants will successfully invade the population currently occupied by the residents and the population will finally becomes* y*-dominant, i.e.* $n(t,x)$ *converges to zero while* $n(t,y)$ *does not converge to zero.*

Note $\theta(w,w) = 0$ for any $w \in X$. The legitimacy of the PIP method depends ultimately on whether there exists a function serving as an invasion exponent for a given dynamical model (COM). More precisely, there are two steps in the construction of invasion exponent.

- To extract a function $\theta(x,y)$ from a given mathematical model of evolution.
- To check whether the function $\theta(x,y)$ satisfies requirements for an invasion exponent in accordance with the original mathematical model.

Generally a model of evolution depends on the type of selection. In the latter sections 1.2 and 1.3, we will introduce models of frequency-dependent selection and density-dependent selection and extract the associated invasion exponents.

1.1.2 The way to use invasion exponent to predict the course of evolution

Under the principle of invasion exponent given in the last subsection, we are going to introduce several important notions associated with an invasion exponent. First in view of the principle of invasion exponent, we have the following definition of "unbeatable" strategy called evolutionarily stable strategy.

Definition 1.1.1 (Evolutionarily stable strategy in [6])**.** *A strategy* $x_* \in X$ *is called an evolutionary stable strategy, ESS for short, if and only if* $\theta(x, y) < 0$ *for any* $y \neq x$*.*

The notion of ESS was originally introduced by Maynard Smith and Price in the framework of evolutionary game theory in [25, 24]. The current definition using the invasion exponent was given by Christiansen [6].

For simplicity, we assume that θ is suitably smooth and $\theta(x, y) = 0$ if and only if $y = x$ and $y = \eta(x)$, where η is a smooth function. Then there exists a smooth function $\xi(x, y)$ such that

$$\theta(x, y) = (y - x)(y - \eta(x))\xi(x, y), \tag{1.1.1}$$

where $\xi(x, y) > 0$ for any $x, y \in X$ or $\xi(x, y) < 0$ for any $x, y \in X$. Although curves $\theta(x, y) = 0$ may include implicit curves as a composition, by virtue of the implicit function theorem and the assumption of small mutation, one can resolve function θ into factors as (1.1.1) without loss of generality.

Definition 1.1.2 (Evolutionarily singular strategy)**.** *A strategy* x_* *is called evolutionarily singular if* $\dfrac{\partial \theta}{\partial y}(x_*, x_*) = 0$*.*

Note that if x_* is ESS, then it is evolutionarily singular. Since we have

$$\frac{\partial \theta}{\partial x}(x_*, x_*) = -\frac{\partial \theta}{\partial y}(x_*, x_*) = -(x_* - \eta(x_*))\xi(x_*, x_*)$$

by (1.1.1), x_* is evolutionary singular if and only if $x_* = \eta(x_*)$.

Except an evolutionarily singular strategy, it is easy to analyze the course of evolution. Namely, let a strategy x_*, which is not evolutionarily singular, dominate the population. The scenario is that a mutation occurs and a new strategy y_* emerges in the proximity of x_*. Precisely we have the following two cases:

Case I: $\dfrac{\partial \theta}{\partial y}(x_*, x_*) > 0$

In this case, $\theta(x, y) \approx (y - x)\frac{\partial \theta}{\partial y}(x_*, x_*)$ around (x_*, x_*). Therefore,

$$\begin{aligned} &x_*\text{-is dominant if } y_* < x_*, \\ &y_*\text{-is dominant if } x_* < y_*. \end{aligned}$$

Hence the evolution proceeds to the direction where the value of the strategy gets larger.

Case II: $\dfrac{\partial \theta}{\partial y}(x_*, x_*) < 0$

Similar discussion as above shows that the evolution proceeds to the direction where the value of the strategy gets smaller. Figure 1.1.2 describes that, using above two results, one can know the direction of the course of evolution graphically.

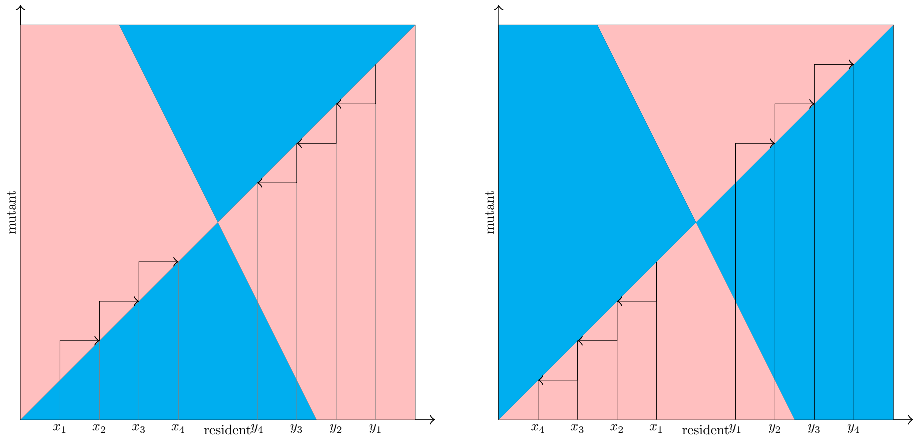

Figure 1.1.1: Trait substitution sequences far from evolutionarily singular strategies. The red and blue areas respectively correspond to the sets $\{\theta(x, y) > 0\}$ and $\{\theta(x, y) < 0\}$. Invasion of a mutant strategy that emerges in the direction of the red area results in substitution of dominant strategy, whereas other mutations result in extinction of the mutants.

The initial study of adaptive dynamics in Section 1.2 dealt with frequency-dependent selection, whereas the currently most popular framework introduced in Section 1.3 deals with density-dependent selection.

Let us briefly explain about the justification of these two invasion exponents. In case that an invasion exponent under frequency-dependent selection is derived from an evolutionary matrix game, it is relatively straight forward to justify the extracted invasion exponent. See Section 1.2. For models based on density-dependent selections, there have been extensive literatures on the extraction of invasion exponent and its justification. See Dercole and Geritz [7] for example. In fact, we are going to extend their work in Chapter 2. We extended one of their results in [22].

We have seen above that $\frac{\partial\theta}{\partial y}(x_*, x_*)$ plays a key role in determining the course of the evolution.

Definition 1.1.3 (Selection gradient)**.** *Define*

$$\lambda(x) = \frac{\partial\theta}{\partial y}(x, x),$$

which is called "selection gradient" at x.

An immediate observation from the above two cases is that if

$$\begin{aligned} &\lambda(x) < 0 \quad \text{if } x_* < x, \\ &\lambda(x) > 0 \quad \text{if } x_* > x, \end{aligned} \tag{1.1.2}$$

for an evolutionarily singular strategy x_*, then no matter where the evolution started, a strategy will converge to x_* as the evolution proceeds. See Figure 1.1.2. Taylor and Jonker [26] introduced the notion of "continuously stable strategy", which is currently called "convergence stable strategy". The current definition using the invasion exponent was given by Christiansen [6].

Definition 1.1.4 (Convergence stable strategy in [6])**.** *A evolutionarily singular strategy x_* is called a convergence stable strategy, CSS for short, if and only if* (1.1.2) *holds.*

Be aware that an evolutionarily singular strategy x_* can be ESS but not CSS or CSS but not ESS. This means that even if x_* is unbeatable, it may not be the goal of the evolution or even if x_* is the ultimate goal of the evolution, it can be replaced by mutants. In the next subsection we are going to classify evolutionary singularity in eight categories by putting attention on the local properties of invasion exponent around an evolutionarily singular strategy.

1.1.3 Classification of the evolution process under PIP method

In this subsection, we introduce a classification of evolutionarily singular strategies as a natural consequence of the principle of invasion exponent.

For this purpose, however, we must introduce the fundamental hypothesis of the PIP method, in which the sign of invasion exponent corresponds only to the success or the failure of invasion by a newly emerged strategy and not to substitution of dominant strategy.

Fundamental hypothesis of the PIP method

(A') *If* $\theta(x,y) < 0$*, mutants will disappear eventually and the population stays* x*-dominant, i.e.* $n(t,y) \to 0$.

(B') *If* $\theta(x,y) > 0$*, mutants will successfully invade the population currently occupied by residents, i.e.* $n(t,y)$ *does not converge to zero.*

(C') *If* $\theta(x,y) > 0$ *and* $\theta(y,x) < 0$*, the mutation is not only successful but also results in the substitution of dominant strategy from* x *to* y*, i.e.* $n(t,y)$ *remains positive while* $n(t,x) \to 0$.

(D') *If* $\theta(x,y) > 0$ *and* $\theta(y,x) > 0$*, the mutation is successful but does not results in the substitution of dominant strategy from* x *to* y*. The residents and the mutants will coexist with each other, i.e.* $n(t,x)$ *and* $n(t,y)$ *remain positive.*

Note that, unless strategy x is close to an evolutionarily singular strategy, the condition $\theta(x,y) > 0$ induces $\theta(y,x) < 0$ by virtue of the assumption of small mutational step, and hence substitution of dominant strategy from x to y.

Although the evolutionary singularity has been classified in the history of adaptive dynamics theory, there are still important remained problems to justify the classification corresponding to the process of evolution around x_*. However the justification requires additional model of the occurrence of mutations and analysis of ODE models which are out of the scope of this paper. Thus we are going just to give a piece of introduction for the classification in the following part of this subsection and this thesis deals with the principle of invasion exponent.

The situation may become clearer by considering local and generic versions of ESS and CSS, where the word "generic" means non-degeneracy of differentials. The notion of local ESS was initially introduced and mathematically formulated by Pohley and Thomas [23]. The current definitions of local ESS and local CSS using the invasion exponent are due to Christiansen [6].

Definition 1.1.5 (Local ESS and local CSS in [6])**.** *Let* x_* *be an evolutionarily singular strategy.*

(1) The strategy x_* is said to be local ESS if and only if $\dfrac{\partial^2\theta}{\partial y^2}(x_*, x_*) < 0$.
(2) The strategy x_* is said to be local CSS if and only if $\lambda'(x_*) < 0$, where $\lambda'(x) = \dfrac{d\lambda}{dx}(x)$.

At an evolutionarily singular strategy x_*, it follows that

$$\begin{aligned}
\frac{\partial^2\theta}{\partial x^2}(x_*, x_*) &= 2\eta'(x_*)\xi(x_*, x_*) \\
\frac{\partial^2\theta}{\partial y^2}(x_*, x_*) &= 2\xi(x_*, x_*) \\
\frac{\partial^2\theta}{\partial x \partial y}(x_*, x_*) &= -(1 + \eta'(x_*))\xi(x_*, x_*)
\end{aligned}$$

and hence

$$\lambda'(x_*) = (1 - \eta'(x_*))\xi(x_*, x_*).$$

Immediately we have the following proposition.

Proposition 1.1.6. *Let x_* be an evolutionarily singular strategy.*
(1) x_* is local ESS if and only if $\xi(x_*, x_*) < 0$.
(2) x_* is local CSS if and only if $(1 - \eta'(x_*))\xi(x_*, x_*) < 0$.

Recall that the first argument is the strategy of residents and the second argument is that of mutants. Due to this non-symmetric nature of an invasion exponent, even if a strategy x_* is local ESS and local CSS as the strategy of residents, x_* itself may not be successful as the strategy of mutants. Moreover it can occur that $\theta(x, y) > 0$ and $\theta(y, x) > 0$ simultaneously. In these respects, notice first that if $\theta(y, x_*) > 0$ for any $y \in X$, then strategy x_* can always play the role of a strategy of successful mutant. A local version of this is the condition $\frac{\partial^2\theta}{\partial x^2}(x_*, x_*) < 0$, since $\theta(x_*, x_*) = 0$ and $\frac{\partial\theta}{\partial x}(x_*, x_*) = 0$. Notice again that if $\theta(x, y) > 0$ and $\theta(y, x) > 0$ for some $x, y \in X$ close to x_* is positive, then both of mutant strategy y of residents x and mutant strategy x of residents y are successful. A local version of this is that the second derivative of θ at (x_*, x_*) along the secondary diagonal $y - x_* = -(x - x_*)$ is positive, i.e.

$$\left.\frac{d^2}{dx^2}\theta(x, -x + 2x_*)\right|_{x = x_*} > 0.$$

In view of the above criteria, since we have

$$\begin{aligned}\frac{d^2}{dx^2}\theta(x,-x+2x_*)\bigg|_{x=x_*} &= \frac{\partial^2\theta}{\partial x^2}(x_*,x_*) - 2\frac{\partial^2\theta}{\partial x\partial y}(x_*,x_*) + \frac{\partial^2\theta}{\partial y^2}(x_*,x_*) \\ &= 4(1+\eta'(x_*))\xi(x_*,x_*),\end{aligned} \tag{1.1.3}$$

evolutionarily singular strategies can be classified into four classes according as the value of $\eta'(x_*)$. Namely $\eta'(x) < -1$, $-1 < \eta'(x) < 0$, $0 < \eta'(x) < 1$ and $1 < \eta'(x)$. Moreover, there are the dichotomies determined by the sign of $\xi(x_*,x_*)$. Considering these two criteria, we can classify an evolutionarily singular strategy into eight categories as follows.

(a) x_* is not local ESS nor local CSS, and thus it is so-called evolutionary repeller. However x_* itself can invade as a mutant into a population whose strategy is close to x_*. There exists a pair of two similar strategies x and y close to x_* such that they coexist in a same population.

(b) x_* is not local ESS but local CSS, and thus it is so-called evolutionary branching point. x_* itself can invade as a mutant into a population whose strategy is close to x_*. There exists a pair of two similar strategies x and y close to x_* such that they coexist in a same population.

(c) x_* is local ESS and local CSS, and thus it is so-called evolutionary attractor. x_* itself can also invade as a mutant into a population whose strategy is close to x_*. There exists a pair of two similar strategies x and y close to x_* such that they coexist in a same population.

(d) x_* is local ESS and local CSS, and thus it is so-called evolutionary attractor. x_* itself can also invade as a mutant into a population whose strategy is close to x_*. However coexistence never occur around x_*, that is, one of two groups ends up with extinction and the other occupies the population.

(e) x_* is local ESS and local CSS, and thus it is so-called evolutionary attractor. However x_* itself can not invade as a mutant into a population whose strategy is close to x_*, and coexistence never occur around x_*, that is, one of two groups ends up with extinction and the other occupies the population.

(f) x_* is local ESS but not local CSS, and thus it is so-called the garden of Eden. Moreover x_* can not invade into other populations and never coexist with another strategies, that is, the group having strategy x_* always ends up with extinction.

(g) x_* is not local ESS nor local CSS, and thus it is so-called evolutionary repeller. Moreover x_* itself can not invade as a mutant into other population and coexistence never occur around x_*, that is, the group having strategy x_* always ends up with extinction.

(h) x_* is not local ESS nor local CSS, and thus it is so-called evolutionary repeller. Moreover x_* itself can not invade as a mutant into other population. However coexistence can occur around x_*. However there exists a pair of two similar strategies x and y close to x_* such that they coexist in a same population..

This classification was originally due to Geritz et al. in [13] into the following eight types (a) – (h) as shown in Table and Figure 1.1.3.

	$\eta'(x_*) < -1$	$-1 < \eta'(x_*) < 0$	$0 < \eta'(x_*) < 1$	$1 < \eta'(x_*)$
$\xi(x_*, x_*) > 0$	(g)	(h)	(a)	(b)
$\xi(x_*, x_*) < 0$	(c)	(d)	(e)	(f)

Table 1.1: Classification of evolutionary singularity w.r.t. the values of $\eta'(x_*)$ and $\xi(x_*, x_*)$. See also Figure 1.1.3 to know the structures of $\theta(x, y)$ around x_*.

In particular, if an evolutionarily singular strategy x^* is CSS and ESS, x^* is called *evolutionary attractor*, which should stand for an attracting point of the course of evolution. In case (c), however, the intersection of the sets $\{\theta(x, y) > 0\}$ and $\{\theta(y, x) > 0\}$ is not empty and hence, by the hypothesis of the PIP method, there exists a pair (x, y) around (x^*, x^*) such that the two strategies coexist. Thus we need to construct a model of evolution in a dimorphic population to check whether or not the case (c) implies that x^* is an attracting point of evolution even in the dimorphic population. In this thesis, however, we do not deal with this kind of problems so that we concentrate on the justification that we mentioned in the last subsection.

In the following sections of this chapter, we will review how the invasion exponents are derived under frequency-dependent selection in Section 1.2 and under density-dependent selection in Section 1.3.

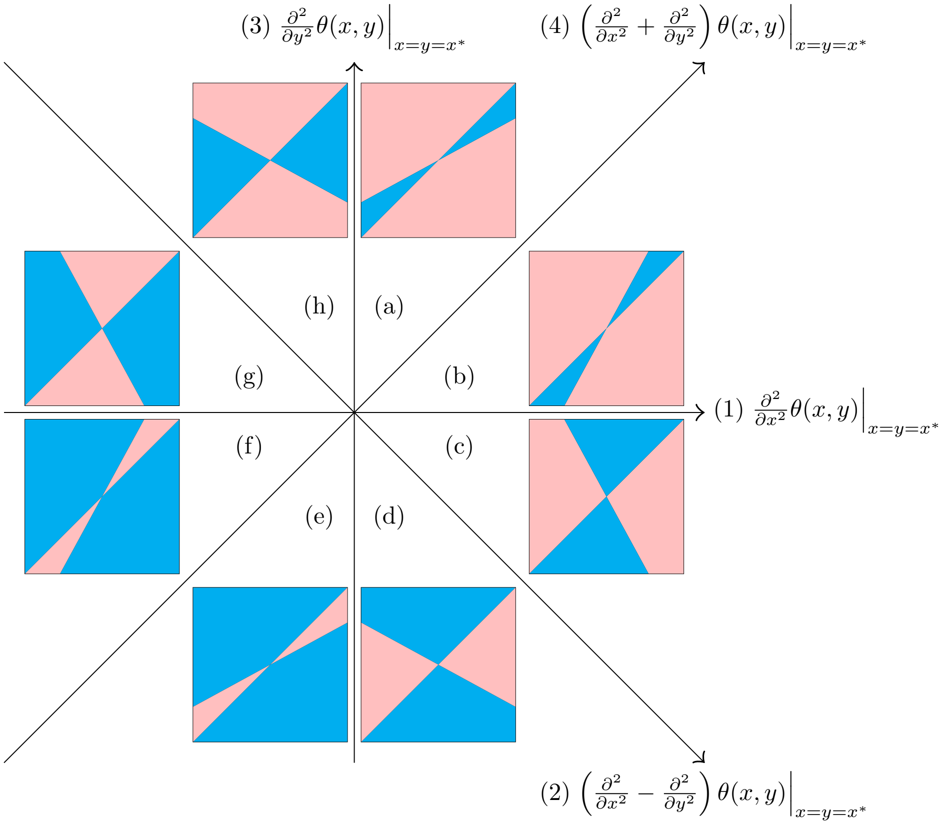

Figure 1.1.2: Evolutionarily singular strategies are classified in terms of the four criteria. The blue areas stand for the sets $\{\theta(x,y)<0\}$ where the red areas for $\{\theta(x,y)>0\}$.

1.2 Invasion exponent under a frequency-dependent selection model

In this section we will introduce the invasion exponent under a frequency-dependent selection model in the context of matrix game theory. The notion of adaptive dynamics was proposed by Nowak in [21], which was discussed in the context of evolutionary game theory. Thus, for the purpose of this section, we should start at introduction of standard game theory and evolutionary game theory.

1.2.1 Evolutionary game theory and invasion exponent

Evolutionary game theory was developed by Maynard Smith and Price[25] to investigate which distribution on strategy set is stable in the framework of the game theory. In this subsection we construct an invasion exponent in the framework of game theory. Let us start by introduction of the standard game theory by Neumann and Morgenstern [20].

A symmetric game is a triplet (N, S, A) where N is the number of players, S is a finite collection of strategies, and A is a real-valued function on S^N, called *payoff matrix*. Here "symmetric" means that all players share the same strategy set. Each element of strategy set is called *pure strategy*.

Let $S = \{s_1, \ldots, s_K\}$. Introducing a probabilistic point of view, we can extend the collection of strategies S to K-dimensional simplex

$$S_K = \left\{ \mathbf{x} = (x_1, \ldots, x_K) \in [0,1]^K \;\middle|\; \sum_{j=1}^{K} x_j = 1 \right\},$$

where the strategy $\mathbf{x} \in S_K$ means that a player takes the strategy s_j in probability x_j for $j = 1, \ldots, K$. Each element of S_K is called a *mixed strategy*, and the real-valued function f on S_K^N defined as follows is called a *payoff function* of strategy $\mathbf{x^{(1)}}$ against $\mathbf{x^{(2)}}, \ldots, \mathbf{x^{(N)}}$:

$$f(\mathbf{x^{(1)}}, \ldots, \mathbf{x^{(N)}}) = \sum_{j=1}^{N} \sum_{i^{(j)}=1}^{K} A(s_{i^{(1)}}, \ldots, s_{i^{(N)}}) x^{(1)}_{i^{(1)}} \cdots x^{(N)}_{i^{(N)}}, \tag{1.2.1}$$

where $\mathbf{x^{(j)}} = (x^{(j)}_1, \ldots, x^{(j)}_K)$ for $j = 1, \ldots, N$.

The study of game theory is, simply speaking, to investigate the distribution of strategies of players when the payoff function of each player is maximized.

Definition 1.2.1 (Nash equilibrium strategy)**.** *A mixed strategy* $\mathbf{x}$ *is said to be Nash equilibrium strategy, NES for short, if inequality*

$$f(\mathbf{x},\mathbf{x},\ldots,\mathbf{x}) \geq f(\mathbf{y},\mathbf{x},\ldots,\mathbf{x})$$

holds for all $\mathbf{y} \in S_K$*. Moreover* $\mathbf{x}$ *is said to be strong NES, if the above equality holds only for* $\mathbf{y} = \mathbf{x}$*.*

Although a game may not have a strong NES, it was proved that all games have an NES by Nash [19].

Theorem 1.2.2 ([19])**.** *For any* N*-player game* (N, S, A)*, there is an NES.*

We shall assume that the population of interest has two strategy $\mathbf{x}$ and $\mathbf{y}$, and that, when an individual meets another individual, the benefits of the two players are determined by the mixed-strategy 2-player game. Precisely, we assume that the payoff function $f(\mathbf{x},\mathbf{y})$ defined as (1.2.1) for $N = 2$, i.e.

$$f(\mathbf{x},\mathbf{y}) = \mathbf{x} \cdot A\mathbf{y},$$

determines the benefits of a player who takes strategy $\mathbf{x}$ and meets a player taking strategy $\mathbf{y}$.

To consider the process of evolution, it is required to consider mutation events. The following assumptions are common in the context of evolutionary game theory.

Assumption 1.2.3. *Let* y *be a mutant strategy of its progenitor* x*.*

- *(A) The initial proportion of mutant is very small.*
- *(B) The new strategy* y *emerging by mutation is very similar to its progenitor strategy* x*, i.e.* $|x - y|$ *is small enough.*

To construct an invasion exponent, we need a model of selection. Taylor & Jonker [26] and Hofbauer & Sigmund [16] introduced a dynamical system of ODEs, called *replicator dynamics*, that describes the course of selection. Let a population have two mixed strategies $\mathbf{x}$ and $\mathbf{y}$ whose proportions in the population are respectively $1 - p \in [0, 1]$ and p. We denote such situation by $Q(p) = ((\mathbf{x}, 1-p), (\mathbf{y}, p))$. Let the payoff function $f(\mathbf{x},\mathbf{y})$ determine the benefits of a player who takes strategy $\mathbf{x}$ and meets a player taking strategy $\mathbf{y}$. Then the expected benefits $W(\mathbf{x}, Q(p))$ and $W(\mathbf{y}, Q(p))$ of strategies $\mathbf{x}$ and $\mathbf{y}$ are given by

$$W(\mathbf{x}, Q(p)) = f(\mathbf{x},\mathbf{x})(1-p) + f(\mathbf{x},\mathbf{y})p,$$
$$W(\mathbf{y}, Q(p)) = f(\mathbf{y},\mathbf{x})(1-p) + f(\mathbf{y},\mathbf{y})p.$$

Letting $\overline{W}(Q(p))$ be the mean value of expected benefits, that is,

$$\overline{W}(Q(p)) = (1-p)W(\mathbf{x}, Q(p)) + pW(\mathbf{y}, Q(p)),$$

the authors of [26, 16] assumed that the time-evolution of proportion p is determined by the difference of the expected benefit of strategy $\mathbf{y}$ and the mean value of expected benefits as follows:

$$\frac{dp}{dt} = p\left(W(\mathbf{y}, Q(p)) - \overline{W}(Q(p))\right) = p(1-p)\left(W(\mathbf{y}, Q(p)) - W(\mathbf{x}, Q(p))\right). \tag{1.2.2}$$

This ODE is called *replicator dynamics.* For (1.2.2), the following theorem is straight forward.

Proposition 1.2.4. *If* $W(\mathbf{x}, Q(p)) < W(\mathbf{y}, Q(p))$ *holds for any* $p \in (0,1)$*, then the equilibrium* $p = 0$ *is unstable and* $p = 1$ *is global attractor, i.e.*

$$\lim_{t \to \infty} p(t) = 1,$$

for any solutions $p(t)$ *of* (1.2.2) *starting at any points in* $(0,1)$.

This proposition means that the group having the strategy x will eventually disappear and the population becomes y-dominant.

In this framework where the process of evolution is described by the replicator dynamics (1.2.2), one can extract an invasion exponent in the following way. For simplicity, we consider one-dimensional real-valued strategies hereafter.

Definition 1.2.5. *The value of function* $\theta(x,y)$ *defined as follows is called invasion exponent of strategy* y *in* x*-dominant population,*

$$\theta(x,y) = \left.\left(W(y, Q(p)) - W(x, Q(p))\right)\right|_{p=0} = f(y,x) - f(x,x).$$

Note that evolutionary stability is stronger than NES but weaker than strong NES. Thus a game could have no ESS.

Let us introduce an example, called hawk-dove game. It gives a model of fight between two opponents over a mate, food or territory. In natural environment, it is often the case that such a fight would stop without giving fatal injury even though one of the fighting party has absolute superiority against the opponent. Such a fighting is called *conventional fighting* in the context of ethology.

Let us consider that there are just two following strategies (H) and (D).

(H) To continue attacking until a player injures its opponent.

(D) To choose the conventional fighting.

We assume that players compete with each other for a benefit G and could obtain a negative benefit $-C$ if both of them take hawk strategy. Precisely, the payoff matrix of this game is assumed to be determined as follows. Evolutionary game theory gives one answer to the ethological question. For the hawk-dove game, the following theorem holds.

	(H)	(D)
(H)	$(G-C)/2$	G
(D)	0	$G/2$

Theorem 1.2.6. *If $C < G$, then the strategy (H) is a strong NES. If $G \geq C$, the game does not have any strong NESs but the strategy G/C that is ESS and CSS.*

Proof. Let strategy $x \in [0,1]$ mean that a player takes the strategy (H) in probability x and the strategy (D) in probability $1-x$. Then, for $x, y \in [0,1]$, we have by definition

$$\theta(x,y) = (y-x)\left(G - \frac{C}{2}(x+y)\right).$$

Thus the strategy G/C is ESS and CSS. □

The above theorem says that, the more powerful weapon the players have, the smaller the value of strategy G/C is and hence the more often the players choose dove-strategy.

1.2.2 Justification of the invasion exponent

The replicator dynamics is constructed by giving the function of expected benefit as a quadratic form of population frequencies. In this section, we are going to explain how the invasion exponent associated with the replicator dynamics is justified.

The standard theory of evolutionary game scopes the replicator dynamics extracted from a matrix game. Hofbauer and Sigmund [16] showed that the replicator dynamics is conjugate, under certain change of coordinates, to Lotka-Volterra competition model

$$\begin{aligned} \dot{n}_1 &= n_1(a - bn_1 - cn_2), \\ \dot{n}_2 &= n_2(d - en_1 - fn_2), \end{aligned} \tag{1.2.3}$$

where $a, b, c, d, e, f \in \mathbb{R}$ are determined by the payoff function $f(x, y)$ for the associated mixed strategy game.

Let us consider the replicator dynamics (1.2.2) associated with a given pure strategy game. Then the following proposition is straight forward as a corollary of Theorem 7.5.1 in [16].

Theorem 1.2.7. *There exists a differentiable, invertible map from* $[0, 1]$ *onto* $\mathbb{R}^2_+$ *mapping the orbits of the replicator equation* (1.2.2) *onto the orbits of a Lotka-Volterra equation* (1.2.3) *for some* $a, b, c, d, e, f \in \mathbb{R}$.

The following theorem is well-known in the field of mathematical ecology, called *competitive exclusion.* See Section 3.3 of [17], for example.

Theorem 1.2.8. *There are three types of qualitative behaviors for solutions of* (1.2.3).

- *Solutions starting in* $\mathbb{R}^2_+$ *converge to an inner attracting equilibrium, whenever*
$$\frac{b}{e} > \frac{a}{d} > \frac{c}{f}.$$
- *Solutions starting in* $\mathbb{R}^2_+$ *converge to an inner attracting equilibrium, whenever*
$$\frac{b}{e} > \frac{a}{d} > \frac{c}{f}.$$
- *There is an inner saddle point and solutions starting in* $\mathbb{R}^2_+$ *converge to either of equilibria on the two axes*
$$\frac{b}{e} < \frac{a}{d} < \frac{c}{f}.$$

(1.2.3) has two equilibria P_1 and P_2 on the n_1 and n_2 axes respectively. Theorem 1.2.8 states that (1.2.3) has four types of global behaviors: P_1 is a global attractor and P_2 is a saddle point; P_1 is a saddle point and P_2 is a global attractor; P_1 and P_2 are saddle points and there is an attractor in the interior of the population state space; P_1 and P_2 is Lyapunov stable and there is a repeller in the interior of the population state space.

Because of this classification, if a mutant y of its progenitor x satisfies $\theta(x, y) > 0$, the mutation results in substitution of dominant strategy of the population $x \to y$. Thus the PIP method associated with an evolutionary game is justified and it can be used to describe the process of evolution in monomorphic populations.

Other types of frequency-dependent selection than the replicator dynamics are embedded into a more general class of population dynamics with density-dependent selection than Lotka-Volterra type. Thus our main result i.e. Theorem 2.2.3 is applicable to justify the PIP method associated with such models.

1.3 Invasion exponent under density-dependent selection

In this section we will introduce another mathematical model of the evolution and the associated invasion exponent. Six years after Nowak's work [21], Metz et al. [18] proposed a mathematical framework to analyze gradual and adaptive evolution driven by not only frequency-dependent selection but also density-dependent selection. This model soon became the main interest in the study of adaptive dynamics. Indeed in the next Chapter, we are going to study questions associated with this particular model.

1.3.1 Dynamical model under density dependent selection and the extraction of invasion fitness

Consider a k-morphic population where the set of traits, i.e. strategies are $x_1, \ldots, x_k$ and let $n_i(t)$ be the population density of the group having the trait x_k. Let the dynamics of population densities $n_i(t)$ of strategies x_i for $i = 1, \ldots, k$ be driven by a dynamical system of differential equations.

$$\frac{d}{dt}\begin{pmatrix} n_1 \\ \vdots \\ n_k \end{pmatrix} = \begin{pmatrix} n_1 f_1^{(k)}(n_1, \ldots, n_k, x_1, \ldots, x_k) \\ \vdots \\ n_k f_k^{(k)}(n_1, \ldots, n_k, x_1, \ldots, x_k) \end{pmatrix},$$

where functions $f_1^{(k)}, \ldots, f_k^{(k)}$ satisfy some biologically natural conditions. In fact, one can consider not only differential but also difference equation model. However, we confine ourselves to ODE model in this paper for simplicity. Moreover, again for simplicity, we present the case $k = 1$ in this section. Consequently, letting $n_r = n_1$, we consider

$$\frac{d}{dt}n_r = n_r f^{(1)}(n_r, x). \tag{1.3.1}$$

Assume that there exists $\widehat{N}_x > 0$ such that

$$\begin{aligned} &f(\widehat{N}_x, x) = 0, \\ &\widehat{N}_x \frac{\partial f^{(1)}}{\partial n_r}(\widehat{N}_x, x) < 0, \\ &\lim_{t \to \infty} n_r(t) = \widehat{N}_x, \end{aligned}$$

for any initial values.

Suppose now that mutants with a strategy y have emerged from the residents, and that the new group having strategy y has negligible population density. Let n_m denote the population density of mutants. Then the competition among strategies x, y is governed by the following system of ODEs:

$$\frac{d}{dt}\begin{pmatrix} n_r \\ n_m \end{pmatrix} = \begin{pmatrix} n_r f_r(n_r, n_m, x, y), \\ n_m f_m(n_r, n_m, x, y) \end{pmatrix}, \tag{1.3.2}$$

where there exists a function $f^{(2)}(n_r, n_m, x, y)$ such that the following conditions hold;

$$f^{(2)}(n_r, n_m, x, y) = f_r(n_r, n_m, x, y) = f_m(n_m, n_r, y, x), \tag{1.3.3}$$
$$f^{(2)}(n_r, 0, x, y) = f^{(1)}(n_r, x), \tag{1.3.4}$$
$$f^{(2)}(n_r, n_m, x, x) = f^{(1)}(n_r + n_m, x), \tag{1.3.5}$$

for any $n_r, n_m \in \mathbb{R}_{\geq 0}$ and $x, y \in X$. These conditions come from the consistency for a biological model.

In this model, a suitable notion of the invasion fitness is defined as

$$\theta(x, y) = f_m(\widehat{N}_x, 0, x, y). \tag{1.3.6}$$

Note that $\theta(x, y) = f_m(\widehat{N}_x, 0, x, y)$ is one of the eigenvalue of the Jacobian.

$$J(x, y) = \begin{pmatrix} \widehat{N}_x \frac{\partial f_r}{\partial n_r}(\widehat{N}_x, 0, x, y) & \widehat{N}_x \frac{\partial f_r}{\partial n_m}(\widehat{N}_x, 0, x, y) \\ 0 & f_m(\widehat{N}_x, 0, x, y) \end{pmatrix}$$

Since $\widehat{N}_x \frac{\partial f_r}{\partial n_r}(\widehat{N}_x, 0, x, y) < 0$, the invasion fitness $\theta(x, y)$ determines the local stability of the equilibrium $(\widehat{N}_x, 0)$.

1.3.2 Justification of the invasion exponent

In view of the observation in the last subsection, the principle of invasion exponent is now equivalent to the statement that $(\widehat{N}_x, 0)$ is locally unstable if and only if $(n_r(t), n_m(t)) \to (0, \widehat{N}_y)$ for any initial values that are sufficiently close to $(\widehat{N}_x, 0)$. Such a statement is not obvious at all, since it means that a local stability determines a global stability. Dercole, Rinldi and Geritz called the statement *invasion-imply-substitution* principle, IIS principle for short, or *invasion-imply-fixation* principle in [12, 8]. See subsection 2.2.2 for further discussion on IIS principle. In this subsection we are going to introduce previous results on IIS principle for various classes of dimorphic population dynamics (1.3.2).

First of all, let us introduce one of the simplest, but most useful type of competition, the Lotka-Volterra competition. For example Bränström et al. [3] dealt with a food-web model that has the effects of Lotka-Volterra competitions, where predation rates and competition kernels are determined by the body sizes of players. Recall Theorem 1.2.8, which says that IIS principle holds for models under the Lotka-Volterra competition.

Secondly we shall introduce an extension of Lotka-Volterra model. Geritz [12] extends the scope of IIS principle from the class of Lotka-Volterra competition to so-called a class of linear environmental feedback-loop. Letting $I(t)$ be the environment factor described as $\sum_{k=1}^{2} G(x_i)n_i(t)$, he says that $I(t)$ *gives the total impact of the entire population on the abundance of the various resources,* that is, the system of ODEs (1.3.2) describing the competition between residents and mutants is assumed to be written as follows;

$$\frac{d}{dt}\begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} n_1 L(x_1, I) \\ n_2 L(x_2, I) \end{pmatrix}, \tag{1.3.7}$$

where functions G and L are assumed to satisfy the following conditions.

(H1) $\frac{\partial L}{\partial x}(x, I)$, $\frac{\partial L}{\partial I}(x, I)$ and $\frac{dG}{dx}(x)$ exist for all $x \in X$ and $I \in \mathbb{R}_+$, and $\frac{\partial L}{\partial I}(x, I)$ is a continuous function of I.

(H2) $X \subset \mathbb{R}^n$ is open and such that for every $x \in X$ there exists a strictly positive hyperbolic attracting steady state $\widehat{n}_x$ of the monomorphic system, that is, $\frac{\partial L}{\partial I}(x, G(x)\widehat{n}_x)G(x) \neq 0$ and $\widehat{n}_x$ is a differentiable function of x.

Let us introduce a set $T_\varepsilon(\widehat{n})$ for $\widehat{n} > 0$ as follows:

$$T_\varepsilon(\widehat{n}) = \left\{(n_1, n_2) \in \mathbb{R}_+^2 \;\middle|\; |n_1 + n_2 - \widehat{n}| \leq \varepsilon\right\}.$$

Then the following theorem holds as a corollary of Proposition 1 in [12].

Theorem 1.3.1. *For every $x \in X$ far from any evolutionarily singular strategy, there exist an $\varepsilon > 0$ and a $\delta > 0$ such that every orbit of* (1.3.7) *starting in the interior of $T_\varepsilon(\widehat{n}_x)$ converges to $(0, \widehat{n}_y)$ as $t \to \infty$ whenever $\theta(x, y) > 0$ and $|y - x| < \delta$.*

Finally let us introduce the most general class for the system of ODEs (1.3.2) in the previous studies. To investigate how much the class of demographic models for the study of evolution can be extended, Brown and Vincent [4, 27] introduced the concept of *generating fitness function*, G-function for short, that is a set of per-capita growth rates of subgroups that have their own strategies. Under the assumption of the existence of G-function, Dercole and Rinaldi [8] state that the IIS theorem holds. See Theorem 2.2.9 for more detail. We are going to discuss about this class of models in the next chapter and to show that the IIS theorem can be also proved as a corollary of our main results.

Chapter 2

Why does invasion imply substitution? – beyond the paradigm of invasion fitness –

In this chapter, we are going to present our results, which has been obtained in [22], on the justification of the invasion exponent associated with the density-dependent selection model introduced in Section 1.3. Recall that the justification is equivalent to "invasion implies substitution principle" in this framework.

2.1 Frameworks and rough description of results

To illuminate our aims and to fix ideas, let us clarify our terminologies and frameworks. The monomorphic system, MMS for short, is the following ordinary differential equation, ODE for short, which describes the time evolution of a population consisting of individuals with a single trait value x,

$$\frac{dn}{dt} = nf_1(n, N, x), \tag{MMS1}$$

where n is the population size and $N \in \mathbb{R}$ is an external environmental factor, which is governed by the ODE

$$\frac{dN}{dt} = q_1(n, N, x) \tag{MMS2}$$

More precisely the monomorphic system (MMS) is the system of ODEs (MMS1) and (MMS2) where $x \in \mathbb{R}$ is a parameter.

The dimorphic system, (DMS) for short, is the system of ODEs describing the time evolution of a population consisting of individuals with two trait values under an external environmental factor N. In this case the population is divided into two groups depending on trait values and those groups compete with each other. Let (n_1, x_1) and (n_2, x_2) be the pairs of the population size and the trait value of two competing groups. In this paper we assume that the growth rate of the population size of the group having trait value x_1 is given by

$$F(n_1, x_1 \mid n_2, x_2, N)$$

and hence

$$\begin{aligned} \frac{dn_1}{dt} &= n_1 F(n_1, x_1 \mid n_2, x_2, N) \\ \frac{dn_2}{dt} &= n_2 F(n_2, x_2 \mid n_1, x_1, N) \end{aligned} \tag{2.1.1}$$

For simplicity, set

$$f_2(n_1, n_2, N, x_1, x_2) = F(n_1, x_1 \mid n_2, x_2, N).$$

Then the complete expression of the dimorphic system is

$$\begin{aligned} \frac{dn_1}{dt} &= n_1 f_2(n_1, n_2, N, x_1, x_2) \\ \frac{dn_2}{dt} &= n_2 f_2(n_2, n_1, N, x_2, x_1) \\ \frac{dN}{dt} &= q_2(n_1, n_2, N, x_1, x_2), \end{aligned} \tag{DMS1}$$

where

$$q_2(n_1, n_2, N, x_1, x_2) = q_2(n_2, n_1, N, x_2, x_1). \tag{DMSS}$$

should hold since the effect of (n_1, x_1) and (n_2, x_2) to the growth of N does not depend on their order. We call the system of ODE's (DMS1) satisfying the symmetry (DMSS) as the dimorphic system, (DMS) for short.

As a model of the competition of two groups within a single species, it is natural to impose two relations between (MMS) and (DMS) :
First, if $n_2 = 0$ in (DMS1), then no competition is present and hence the system is reduced to (MMS). Namely it is required that

$$\begin{aligned} f_2(n_1, 0, N, x_1, x_2) &= F(n_1, x_1 \mid 0, x_2, N) = f_1(n_1, N, x_1) \\ q_2(n_1, 0, N, x_1, x_2) &= q_1(n_1, N, x_1). \end{aligned} \tag{2.1.2}$$

Secondly if the trait values x_1 and x_2 are equal in (DMS1), then it should be reduced to (MMS) with $n = n_1 + n_2$. Mathematically, it is required that

$$\begin{aligned} f_2(n_1, n_2, N, x, x) &= F(n_1, x \mid n_2, x, N) = f_1(n_1 + n_2, N, x) \\ q_2(n_1, n_2, N, x, x) &= q_1(n_1 + n_2, N, x). \end{aligned} \tag{2.1.3}$$

As a whole, our mathematical framework of this paper is the systems of ODEs, (DMS1) and (MMS) with the properties of (2.1.2) and (2.1.3). Such a pair of (MMS) and (DMS) is called a 2-hierarchical system, whose exact definition is as follows.

Definition 2.1.1 (2-hierarchical system)**.** *A pair* $((f_1, q_1), (f_2, q_2))$ *is called a* 2*-hierarchical system, (2HS) for short, if and only if* (f_1, q_1) *is (MMS),* (f_2, q_2) *is (DMS) and the consistency conditions* (2.1.2) *and* (2.1.3) *are satisfied.*

For the sake of simplicity, we are going to assume that for all parameter x, (MMS) has a unique equilibrium point $(\widehat{n}_x, \widehat{N}_x)$ which is a global attractor, i.e. $\lim_{t\to\infty}(n(t), N(t)) = (\widehat{n}_x, \widehat{N}_x)$ for every nonnegative solution $(n(t), N(t))$ of (MMS). (See Assumption 2.2.1 for the precise statement.)

The course of events in this model is as follows: suppose that the population is dominated by residents with a single trait value x_*, i.e. the monomorphic system (MMS) with the parameter x_* stays at the stable equilibrium $(\widehat{n}_{x_*}, \widehat{N}_{x_*})$. At a certain point, a mutation occurs and a small group of mutants with a new trait value x is introduced into the system. Accordingly, the system of interest has been changed to the dimorphic system with parameter x_* and x starting from near the equilibrium $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$, which is not necessarily stable as a dimorphic system. Our main interest is to analyze the global behavior of this dimorphic system (DMS1). In particular, plausible outcomes of our concern are the following three (A), (B) and (C):

(A) The equilibrium $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ is globally stable, i.e. mutants are going to extinct eventually and the system will return to the monomorphic system with the original trait value x_*.

(B) The new trait value x is superior to the original one x_* and eventually mutants will dominate the population. In our framework, this means that the equilibrium $(0, \widehat{n}_x, \widehat{N}_x)$ is globally stable and every solution of (DMS1) starting near the original equilibrium $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ is going to converge to $(0, \widehat{n}_x, \widehat{N}_x)$.

(C) Two trait values x_* and x are going to coexist in certain proportion, i.e. there exists a stable equilibrium $(\widetilde{n}_{x_*}, \widetilde{n}_x, \widetilde{N})$ of (DMS1) such that $\widetilde{n}_{x_*}, \widetilde{n}_x > 0$ and every solution starting near the original equilibrium $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ is going to converge to $(\widetilde{n}_{x_*}, \widetilde{n}_x, \widetilde{N})$.

Our main results are the followings:

(I) First we have established a sufficient condition for the global shift between (A) and (B). To be exact, we introduce the notion of raw invasion fitness $\Theta(n_1, n_2, N, x_1, x_2)$ as the difference between the fitnesses of mutants and residents. i.e.

$$\Theta(n_1, n_2, N, x_1, x_2) = f_2(n_2, n_1, N, x_2, x_1) - f_2(n_1, n_2, N, x_1, x_2) \quad (2.1.4)$$

Note that $\Theta = 0$ on the line segment $L(x_*)$ defined by

$$L(x_*) = \left\{(n_1, n_2, \widehat{N}_{x_*}, x_*, x_*) \,\middle|\, n_1 + n_2 = \widehat{n}_{x_*}, n_1, n_2 \geq 0\right\}. \quad (2.1.5)$$

The "classical" invasion fitness $\theta(\cdot, \cdot)$ turns out to be a special value of our raw invasion fitness as follows:

$$\theta(x_1, x_2) = f_2(0, \widehat{n}_{x_*}, \widehat{N}_{x_*}, x_2, x_1) = \Theta(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*}, x_1, x_2). \quad (2.1.6)$$

Our theorem, Theorem 2.2.3, shows that if

$$\frac{\partial \Theta}{\partial x_2} \text{ is uniformly positive on } L(x_*), \quad (2.1.7)$$

then as x crosses x_*, (B) happens while $x_* < x$ and (A) happens while $x < x_*$. Under our condition (2.1.7), Θ is uniformly positive (resp. negative) around $L(x_*)$ when $x < x_*$ (resp. $x_* < x$). Thus our result matches the intuition that whichever has the higher fitness wins the competition.

(II) Secondly, we are going to show that IIS principle by Dercole and Rinaldi in [8] can be obtained as a corollary of our general result mentioned above. More specifically, we introduce the notion of a trimorphic system, (TMS) for short, which is a system of ODE's describing the competition of tree groups having different trait values. As is the case of 2-hierarchical system, we call a consistent triple of (MMS), (DMS) and (TMS) a 3-hierarchical system, (3HS) for short. Under these terminologies, a careful examination of the discussions by Dercole and Rinaldi [8] yields that their result can be divided into the following two steps:

- If a dimorphic system is a part of 3-hierarchical system, then there exists a generating function associated with the dimorphic system.
- If there exists a generating function associated with a dimorphic system, then IIS principle holds.

The notion of generating function has been introduced by Brown and Vincent in [4] and [27]. In fact, we are going to present a characterization of the existence of generating function in terms of raw invasion fitness Θ. Namely, in Theorem 2.2.10, the existence of associated generating function is shown to be equivalent to the condition that $\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_1)$ only depends on the values of $n_1 + n_2$, N and x_1. In view of (2.1.6), this characterization will lead to IIS principle under the existence of generating function. See Subsection 2.2.2 for details. Furthermore, we are going to present a class of examples showing

$$\begin{aligned}
&\{\text{(DMS) as a part of 3-hierarchical system}\} \\
&\subsetneq \{\text{(DMS) having associated generating function}\} && (1) \\
&= \text{the scope of the method using the invasion fitness} && (2) \\
&\subsetneq \{\text{(DMS) as a part of 2-hierarchical system}\} && (3) \\
&= \text{the scope of the method using the raw invasion fitness.} && (4)
\end{aligned}$$

The inclusion/not equality (1) in the second line is derived from Theorem 2.2.8 and Proposition 2.2.11.
The equality (2) in the third line is concluded by Theorem 2.2.3, 2.2.9 and 2.2.10.
The inclusion/not equality (3) in the fourth line is due to Proposition 2.2.7 and 2.2.13.
The equality (4) in the last line is due to Theorem 2.2.3.
(III) Thirdly, we have obtained a simple class of examples who have no associated generating functions and where IIS principle may fail. Precisely our example is the following 2-hierarchical system:

$$\begin{aligned}
\frac{dn_1}{dt} &= n_1\big(1 - (n_1 + n_2) + (x_2 - x_1)n_2(c - an_1 - bn_2)\big) \\
\frac{dn_2}{dt} &= n_2\big(1 - (n_1 + n_2) + (x_1 - x_2)n_1(c - an_2 - bn_1)\big) \qquad (2.1.8) \\
\frac{dN}{dt} &= N(1 - N).
\end{aligned}$$

Although the third equation is noting to do with the first and second ones, we put it here for the sake of formality to match (2.1.8) with (DMS1). Immediately, one sees $\widehat{N} = 1$. Furthermore since the associated (MMS) is

$$\frac{dn}{dt} = n(1 - n),$$

it follows that $\widehat{n}_x = 1$ for any x. In this class, an associated generating function exists if and only if $a = b$. If

$$(b-c)(a+b-2c) > 0,$$

then we can apply our result in part (I) and show the shift of global stability between the resident dominant and the mutant dominant equilibriums. On the contrary, if

$$(b-c)(a+b-2c) < 0,$$

$x_2 < x_1$ and x_2 is sufficiently close to x_1, then (C) occurs, i.e. there exists a stable equilibrium $(\widetilde{n}_{x_1}, \widetilde{n}_{x_2}, 1)$ such that $\widetilde{n}_{x_1}, \widetilde{n}_{x_2} > 0$ and any solution starting from near the resident dominant equilibrium $(1, 0, 1)$ converges to $(\widetilde{n}_{x_1}, \widetilde{n}_{x_2}, 1)$. Consequently, IIS principle fails in this example. Note that due to the above result (II), this won't happen under the existence of a generating function. See Subsection 2.2.3 for exact statements.

2.2 Main results

In this section, we are going to give exact statements of our results in three subsections according as the rough description (I), (II) and (III) in the introduction. In Subsection 2.2.1, first we provide the notion of shift of global stability called SU-shift and US-shift, where the symbol "S" and "U" stand for "stable" and "unstable" respectively, and give a sufficient condition for shifts of stability as we outlined in (I). In Subsection 2.2.2, assuming the existence of generating function, we obtain IIS principle originally proven by Dercole and Rinaldi as a corollary of Theorem 2.2.3 in Subsection 2.2.1 by using certain characterization of the existence of generating function obtained in Theorem 2.2.10. In the last subsection 2.2.3, we give a simple class of examples where we observe all the variety of plausible outcomes (A), (B) and (C) in the introduction.

Our domain for (MMS) is

$$\mathcal{U}_1 = \{(n, N, x) \mid n \in \mathbb{R}_+, N \in \mathbb{R}, x \in \mathbb{R}\},$$

where the variables n, N, and x represent a population size, an external environmental factor and a trait value respectively. The external environmental factor may represent amount of available nutrition, population size of a predator species and so on. The functions f_1 and q_1 are assumed to be smooth, to be exact, C^∞ in a neighborhood of $\mathcal{U}_1$, i.e. they can be extended to open neighborhoods of $\mathcal{U}_1$ and are C^∞ in their extended domains.

In the similar manner, the domain for (DMS) is

$$\mathcal{U}_2 = \{(n_1, n_2, N, x_1, x_2) \mid n_1, n_2 \in \mathbb{R}_+, N, x_1, x_2 \in \mathbb{R}\},$$

where n_1 (resp. n_2) represents a population size of individuals with a trait value x_1 (resp. x_2) and N represents an external environmental factor. Note that the first trait value x_1 belongs to residents and the second one belongs to mutants in our model. The functions f_2 and q_2 are assumed to be sufficiently smooth, to be exact, C^∞ in a neighborhood of $\mathcal{U}_2$, i.e. they can be extended open neighborhoods of $\mathcal{U}_2$ and are C^∞ on their extended domains.

Furthermore, for the sake of simplicity of statements, we assume the following property.

Assumption 2.2.1. *For any $x \in \mathbb{R}$, there exists a global attractor $(\widehat{n}_x, \widehat{N}_x)$ such that any solution of (MMS), $(n(t), N(t))$ converges to $(\widehat{n}_x, \widehat{N}_x)$ as $t \to \infty$. Moreover, $(\widehat{n}_x, \widehat{N}_x)$ is hyperbolic and the real parts of all the eigenvalues of the linearization of (MMS) at $(\widehat{n}_x, \widehat{N}_x)$,*

$$\begin{pmatrix} \widehat{n}_x \dfrac{\partial f_1}{\partial n}(\widehat{n}_x, \widehat{N}_x, x) & \widehat{n}_x \dfrac{\partial f_1}{\partial N}(\widehat{n}_x, \widehat{N}_x, x) \\ \\ \dfrac{\partial q_1}{\partial n}(\widehat{n}_x, \widehat{N}_x, x) & \dfrac{\partial q_1}{\partial N}(\widehat{n}_x, \widehat{N}_x, x) \end{pmatrix} \tag{2.2.1}$$

are negative.

The second assumption about eigenvalues of the linearization ensures the local stability of the equilibrium $(\widehat{n}_x, \widehat{N}_x)$.

Even without the assumption that $(\widehat{n}_{x_*}, \widehat{N}_{x_*})$ is a global attractor, if the eigenvalues of (2.2.1) has negative real parts, then our theorems in this paper still hold with some (rather complicated but non-essential) modifications in the statements.

2.2.1 Shifts of stability

The shift of global stability in this paper means the global transition between the resident dominant state and the mutant dominant state as the trait value of mutants varies around the trait value of residents. Throughout this subsection, we consider a 2-hierarchical system $(f_1, q_1), (f_2, q_2)$ satisfying Assumption 2.2.1. To present an explicit statement, we need the notion of a tubular neighborhood $S_\epsilon(x_*)$ of $L(x_*)$ defined as

$$S_\epsilon(x_*) = \left(\bigcup_{(n_1,n_2,\widehat{N}_{x_*},x_*,x_*)\in L(x_*)} B((n_1,n_2,\widehat{N}_{x_*}),\epsilon) \right) \cap \left([0,\infty)^2 \times \mathbb{R}\right),$$

where $B(x,\epsilon)$ is a Euclidean ball given by $\{y \mid |x-y| < \epsilon\}$.

Definition 2.2.2. *Let $x_* \in \mathbb{R}$. We say that SU-shift (resp. US-shift) occurs at x_* if there exist $\epsilon, \delta > 0$ such that if $\{(n_1(t), n_2(t), N(t))\}_{t\geq 0}$ is a solution of (DMS) and $(n_1(0), n_2(0), N(0)) \in S_\epsilon(x_*)$, then*

$$\lim_{t\to\infty}(n_1(t), n_2(t), N(t)) = (\widehat{n}_{x_*}, 0, \widehat{N}_{x_*}) \tag{S}$$

whenever $x_1 = x_*$ and $x_2 \in (x_* - \delta, x_*)$ (resp. $x_2 \in (x_*, x_* + \delta)$) and

$$\lim_{t\to\infty}(n_1(t), n_2(t), N(t)) = (0, \widehat{n}_{x_2}, \widehat{N}_{x_2}) \tag{U}$$

whenever $x_1 = x_*$ and $x_2 \in (x_*, x_* + \delta)$ (resp. $x_2 \in (x_* - \delta, x_*)$).

Recall that the trait values x_* and x_2 belong to residents and mutants respectively. The statement (S) (resp. (U)) means that any solution starting from near $L(x_*)$ converges to the resident (resp. mutant) dominant state $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ (resp. $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$) as $t \to \infty$. Thus SU-shift and US-shift at x_* are global qualitative transitions between (S) and (U) with the critical value x_*.

The following theorem gives a sufficient condition for shift of global stability.

Theorem 2.2.3. *Let $x_* \in \mathbb{R}$. SU-shift (resp. US-shift) occurs at x_* if the following condition* (2.2.2) *(resp.* (2.2.3)*) holds;*

$$\inf_{(n_1,n_2,N,x_1,x_2)\in L(x_*)} \frac{\partial\Theta}{\partial x_2}(n_1,n_2,N,x_1,x_2) > 0, \tag{2.2.2}$$

$$\sup_{(n_1,n_2,N,x_1,x_2)\in L(x_*)} \frac{\partial\Theta}{\partial x_2}(n_1,n_2,N,x_1,x_2) < 0. \tag{2.2.3}$$

We will prove this theorem in A.1. Here we give a rough idea why it is true. Note that $\Theta = 0$ if $x_2 = x_*$. Hence

$$\Theta \approx (x_2 - x_*)\frac{\partial\Theta}{\partial x_2} \tag{2.2.4}$$

if x_2 is sufficiently close to x_*. Suppose that (2.2.2) is true. If $x_2 < x_*$, then $\Theta < 0$ in a small neighborhood of $L(x_*)$, i.e. $S_\epsilon(x_*)$. Namely, the fitness of residents is uniformly higher than that of mutants. Consequently, residents will be dominant. If $x_2 > x_*$, then everything becomes opposite and so we have SU-shift.

2.2.2 IIS principle

In this subsection, we are going to show that IIS principle can be shown as a corollary of our Theorem 2.2.3. As we have mentioned in the introduction, the essential claim of IIS principle is that the local stability of the resident dominant equilibrium determines the global stability of both the resident dominant and the mutant dominant equilibriums. To begin with, let us make an observation on the local stability of the resident dominant equilibrium $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ of (DMS) with parameters (x_*, x_2). One can easily see that the eigenvalues of the linearization of (DMS) at $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ are given by the eigenvalues of (2.2.1) and the invasion fitness $\theta(x_*, x_2)$. By Assumption 2.2.1, the sign of $\theta(x_*, x_2)$ determines the local stability of $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$, i.e. if $\theta(x_*, x_2) > 0$ (reps. $\theta(x_*, x_2) < 0$), then it is locally unstable (resp. stable).

At this point, we are going to revisit the original proof of IIS principle by Dercole and Rinaldi in [8, Appendix B]. They started with a 2-hierarchical system and assumed the existence of a trimorphic system behind, which has turned out to be the key to fill the gap between local and global stabilities.

A trimorphic system is a system of ODE's representing competition of three groups inside a single species having three (different) trait values. As (DMS), let (n_i, x_i) for $i = 1, 2, 3$ be the pair of the population size and the trait value of i-th group and let N be an external environmental factor. Suppose $\{i, j, k\} = \{1, 2, 3\}$. Then it is natural to assume that the fitness of a group i is effected only by the current state of itself, (n_i, x_i), the current state of the opponent groups, $\{(n_j, x_j), (n_k, x_k)\}$, and the external environmental factor N including possible effect of another living organism. As a result, the fitness of the group having the trait value x_i must be written as

$$F_*(n_i, x_i \mid \{(n_j, x_j), (n_k, x_k)\}, N). \qquad (2.2.5)$$

Consequently, the time evolution of the group i is governed by

$$\frac{dn_i}{dt} = n_i F_*(n_i, x_i \mid \{(n_j, x_j), (n_k, x_k)\}, N).$$

By the same line of reasoning, we assume that the growth rate of the external environmental factor N is given by

$$H(N \mid \{(n_i, x_i), (n_j, x_j), (n_k, x_k)\}). \tag{2.2.6}$$

Consequently the time evolution of N is governed by

$$\frac{dN}{dt} = H(N \mid \{(n_i, x_i), (n_j, x_j), (n_k, x_k)\})$$

Hence if we introduce functions

$$\begin{aligned} f_3 &: (\mathbb{R}_+)^3 \times \mathbb{R} \times \mathbb{R}^3 \to \mathbb{R}, \\ q_3 &: (\mathbb{R}_+)^3 \times \mathbb{R} \times \mathbb{R}^3 \to \mathbb{R}, \end{aligned}$$

as

$$f_3(n_1, n_2, n_3, N, x_1, x_2, x_3) = F_*(n_1, x_1 \mid \{(n_2, x_2), (n_3, x_3)\}, N),$$

and

$$q_3(n_1, n_2, n_3, N, x_1, x_2, x_3) = H(N \mid \{(n_1, x_1), (n_2, x_2), (n_3, x_3)\}),$$

then the full equation of the trimorphic system is

$$\begin{aligned} \frac{dn_1}{dt} &= n_1 f_3(n_1, n_2, n_3, N, x_1, x_2, x_3), \\ \frac{dn_2}{dt} &= n_2 f_3(n_2, n_3, n_1, N, x_2, x_3, x_1), \\ \frac{dn_3}{dt} &= n_3 f_3(n_3, n_1, n_2, N, x_3, x_1, x_2), \\ \frac{dN}{dt} &= q_3(n_1, n_2, n_3, N, x_1, x_2, x_3). \end{aligned} \tag{2.2.7}$$

Additionally, since the values of F_* given by (2.2.5) and H given by (2.2.6) are independent of the order of j and k and the order of i, j and k respectively, it is natural to assume that

$$f_3(n_i, n_j, n_k, N, x_i, x_j, x_k) = f_3(n_i, n_k, n_j, N, x_i, x_k, x_j) \tag{2.2.8}$$

and

$$q_3(n_1, n_2, n_3, N, x_1, x_2, x_3) = q_3(n_i, n_j, n_k, N, x_i, x_j, x_k), \tag{2.2.9}$$

where (i, j, k) is an arbitrary permutation of $(1, 2, 3)$.

Definition 2.2.4 (Trimorphic system). *Write* $\mathcal{U}_3 = (\mathbb{R}_+)^3 \times \mathbb{R} \times \mathbb{R}^3$. *A system of ODE's* (2.2.7) *is called a trimorphic system, (TMS) for short, if and only if* f_3 *and* q_3 *are* C^∞ *function defined on a neighborhood of* $\mathcal{U}_3$ *and satisfy* (2.2.8) *and* (2.2.9) *on* $\mathcal{U}_3$ *respectively.*

There are natural consistency conditions (ET) and (CT) between (DMS) and (TMS) as was the case between (MMS) and (DMS).
(ET) Extinction of a trait value: If $n_3 = 0$, then the third group is no longer existent and the system becomes dimorphic with the groups of trait values x_1 and x_2. Mathematically, this requires

$$f_3(n_1, n_2, 0, N, x_1, x_2, x_3) = f_2(n_1, n_2, N, x_1, x_2) \tag{2.2.10}$$

and

$$q_3(n_1, n_2, 0, N, x_1, x_2, x_3) = q_2(n_1, n_2, N, x_1, x_2). \tag{2.2.11}$$

(CT) Coincidence of trait values: In case two trait values coincide, then two groups sharing the same trait value behave as one. Hence the system becomes dimorphic. Mathematically this requires

$$f_3(n_1, n_2, n_3, N, x_1, x_1, x_3) = f_2(n_1 + n_2, n_3, N, x_1, x_3), \tag{2.2.12}$$

$$f_3(n_1, n_2, n_3, N, x_1, x_2, x_2) = f_2(n_1, n_2 + n_3, N, x_1, x_2) \tag{2.2.13}$$

and

$$q_3(n_1, n_2, n_3, N, x_1, x_1, x_2) = q_2(n_1 + n_2, n_3, N, x_1, x_3). \tag{2.2.14}$$

There are other variations like the case $n_1 = 0$ or $x_3 = x_1$ but the associated mathematical relation are all deduced form the above requirements in (CT) and (ET) due to the symmetries (2.2.8) and (2.2.9).

The conditions in (ET) and (CT) ensure the consistency between (DMS) and (TMS).

Now, we fix terminologies without ambiguity.

Definition 2.2.5.
(1) A triple $((f_1, q_1), (f_2, q_2), (f_3, q_3))$ *is said to be a* 3*-hierarchical system, (3HS) for short, if and only if* $((f_1, q_1), (f_2, q_2))$ *is a (2HS),* (f_3, q_3) *is a (TSM) and all the consistency conditions* (2.2.10), (2.2.11), (2.2.12), (2.2.13) *and* (2.2.14) *are satisfied for any* $(n_1, n_2, n_3, N, x_1, x_2, x_3) \in \mathcal{U}_3$.
(2) $f \in C^\infty(\mathcal{U}_2)$ *is said to be a part of (2HS) if and only if there exists a (2HS),* $((f_1, q_1), (f_2, q_2))$, *such that* $f = f_2$.
(3) $f \in C^\infty(\mathcal{U}_2)$ *is said to be a part of (3HS) if and only if there exists a (3HS),* $((f_1, q_1), (f_2, q_2), (f_3, q_3))$, *such that* $f = f_2$.

There is one more notion playing a key role, which is the notion of generating function introduced by Brown and Vincent in [4] and [27].

Definition 2.2.6 (Generating function)**.** *(1) A function* $G : \mathcal{U}_2 \times \mathbb{R} \to \mathbb{R}$ *which is* C^∞ *in a neighborhood of* $\mathcal{U}_2 \times \mathbb{R}$*, is called a generating function if and only if it satisfies the following conditions (G1),(G2) and (G3).*
(G1) For any $n_1 > 0$*,* $x_1, x_2 \in \mathbb{R}$ *and* $N \in \mathbb{R}$*,*

$$G(n_1, 0, N, x_1, x_2, x_1) = G(n_1, 0, N, x_1, x_1, x_1) \tag{2.2.15}$$

(G2) For any $s > 0$*,* $r_1, r_2 \in [0, 1]$ *and* $N, x, y \in \mathbb{R}$*,*

$$G((1 - r_1)s, r_1 s, N, x, x, y) = G((1 - r_2)s, r_2 s, N, x, x, y) \tag{2.2.16}$$

(G3) For any $(n_1, n_2, N, x_1, x_2, y) \in \mathcal{U}_2 \times \mathbb{R}$*,*

$$G(n_1, n_2, N, x_1, x_2, y) = G(n_2, n_1, N, x_2, x_1, y). \tag{2.2.17}$$

(2) $f \in C^\infty(\mathcal{U}_2)$ *is said to have an associated generating function if and only if there exists a generating function* $G : \mathcal{U}_2 \times \mathbb{R} \to \mathbb{R}$ *such that*

$$f(n_1, n_2, N, x_1, x_2) = G(n_1, n_2, N, x_1, x_2, x_1)$$

for any $(n_1, n_2, N, x_1, x_2) \in \mathcal{U}_2$*. In this situation,* G *is called a generating function associated with* f*.*

As a model, the variables n_1, n_2, N, x_1, x_2 have the same roles as before. The sixth variable y has been called virtual strategy in [4] and [27].

The conditions (G1), (G2) and (G3) correspond to the conditions (P1), (P2) and (P3) in Dercole and Geritz [7], where their definition of a generating function contains an additional condition (P4).

Let G be a generating function. If f_1 and f_2 are defined by

$$f_2(n_1, n_2, N, x_1, x_2) = G(n_1, n_2, N, x_1, x_2, x_1) \tag{2.2.18}$$

and

$$f_1(n_1, x_1) = G(n_1, 0, N, x_1, x_1, x_1), \tag{2.2.19}$$

then, with appropriate choice of q_1 and q_2, $q_1 \equiv 0$ and $q_2 \equiv 0$ for example, $((f_1, q_1), (f_2, q_2))$ is a (2HS). Thus we have the following fact.

Proposition 2.2.7. *If* $f \in C^\infty(\mathcal{U}_2)$ *has an associated generating function, then* f *is a part of (2HS).*

In our terminologies, two steps of arguments by Dercole and Rinaldi in [8] mentioned in the introduction can be stated as the following two theorems, Theorems 2.2.8 and 2.2.9.

Theorem 2.2.8 (Dercole and Rinaldi[8])**.** *If* $f \in C^\infty(\mathcal{U}_2)$ *is a part of (3HS), then* f *has an associated generating function.*

The following proof of the above theorem is based on the idea of Dercole and Rinaldi.

Proof. Let $((f_1, q_1), (f_2, q_2), (f_3, q_3))$ be a (3HS) and $f = f_2$. Set

$$G(n_1, n_2, N, x_1, x_2, y) = f_3(0, n_1, n_2, N, y, x_1, x_2).$$

Then by (2.2.12),

$$G(n_1, n_2, N, x_1, x_2, x_1) = f_3(0, n_1, n_2, N, x_1, x_1, x_2) = f_2(n_1, n_2, N, x_1, x_2).$$

Therefore, by (2.1.2)

$$G(n_1, 0, N, x_1, x_2, x_1) = f_2(n_1, 0, N, x_1, x_2) = f_1(n_1, x_1)$$

and hence we have (G1). By (2.2.13), it follows that

$$\begin{aligned} G(rs, (1-r)s, N, x_1, x_1, y) &= f_3(0, (1-r)s, rs, N, y, x_1, x_1) \\ &= f_2(0, s, N, y, x_1). \end{aligned}$$

This immediately implies (G2). Moreover, we have (G3) by (2.2.8). Thus we have shown that G is a generating function associated with f. □

Theorem 2.2.9 (Dercole and Rinaldi's IIS principle)**.** *Let* $((f_1, q_1), (f_2, q_2))$ *be a (2HS) and* f_2 *have an associated generating function. If*

$$\frac{\partial \theta}{\partial x_2}(x_*, x_*) \tag{2.2.20}$$

is positive (resp. negative), then SU-shift (resp. US-shift) occurs at x_**.*

Let us clarify how this theorem is deduced from our main theorem, Theorem 2.2.3. By (2.1.6), it follows that

$$\frac{\partial \theta}{\partial x_2}(x_*, x_*) = \frac{\partial \Theta}{\partial x_2}(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*}, x_*, x_*). \tag{2.2.21}$$

Since $\theta(x_*, x_*) = 0$, we see that

$$\theta(x_*, x_2) \approx (x_2 - x_*)\frac{\partial \theta}{\partial x_2}(x_*, x_*) = (x_2 - x_*)\frac{\partial \Theta}{\partial x_2}(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*}, x_*, x_*). \tag{2.2.22}$$

So, in case $\frac{\partial \theta}{\partial x_2}(x_*, x_*) > 0$ for example, the locally stability of $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*})$ changes from being stable to being unstable as x_2 crosses x_* form below. Comparing this with (2.2.4) and our theorem 2.2.3, one can clearly recognize the gap between the local and the global stabilities. Namely, the shift of global stability is determined by the sign of $\frac{\partial \Theta}{\partial x_2}$ on the whole line segment $L(x_*)$ while the change of local stability is determined by that of the one point $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*}, x_*, x_*)$ in $L(x_*)$.

So, how is it possible that the sign of a value at one point can determine that of the whole points in $L(x_*)$? Our answer is simple: if f_2 has an associated generating function, then the value of $\frac{\partial \Theta}{\partial x_2}$ is constant on $L(x_*)$ so that the value at one point $(\widehat{n}_{x_*}, 0, \widehat{N}_{x_*}, x_*, x_*)$ is the values of the whole points in $L(x_*)$. Actually such a property is the essence of generating function as the next theorem says.

Theorem 2.2.10. *Let $((f_1, q_1), (f_2, q_2))$ be a (2HS). Then f_2 has an associated generating function if and only if $\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_1)$ only depends on the values of $n_1 + n_2$, N and x_1.*

This theorem will be proven in A.3.

Given this theorem, it is now clear that Dercole and Rinaldi's IIS principle is an immediate corollary of our main theorem, Theorem 2.2.3 as follows.

Proof of Theorem 2.2.9. Assume that $((f_1, q_1), (f_2, q_2))$ is a (2HS) and f_2 has an associated generating function. Then by Theorem 2.2.10, it follows that $\frac{\partial \Theta}{\partial x_2}$ is constant on $L(x_*)$. Hence it coincides with $\frac{\partial \theta}{\partial x_2}(x_*, x_*)$. Now Theorem 2.2.3 immediately yields the desired conclusions. $\square$

At this point, we have fulfilled our original aim of this section, which has been to show that the original IIS principle of Dercole and Rinaldi can be obtained as a corollary of our main theorem. There still remain, however, intriguing questions concerning generating functions. One of them is the converse of Theorem 2.2.8: if f has an associated generating function, then is f a part of (3HS)? This turns out to be false since we have the following counterexample.

Proposition 2.2.11. *Define*

$$\begin{aligned} &f(n_1, n_2, N, x_1, x_2) \\ &\qquad = 1 - (n_1 + n_2) + (x_2 - x_1)n_2\big(\alpha\big(n_1\big)^2 + \beta n_1 n_2 + \gamma(n_2)^2\big). \end{aligned} \tag{2.2.23}$$

Then f is a part of (2HS) for any α, β and γ. Furthermore,
(1) f has an associated generating function if and only if $\beta + \gamma = 3\alpha$.
(2) f is a part of (3HS) if and only if $\alpha = \gamma$ and $\beta = 2\alpha$.

So, if $\alpha = 1, \beta = 0$ and $\gamma = 3$ for example, then f has an associated generating function but it is not a part of (3HS). The key fact to show Proposition 2.2.11 is the following proposition.

Theorem 2.2.12. *A smooth function $f : \mathcal{U}_2 \to \mathbb{R}$ is a part of (3HS) if and only if there exist smooth functions $\xi, f_* : \mathcal{U}_1 \to \mathbb{R}$ and $\rho : \mathcal{U}_2 \to \mathbb{R}$ satisfying*

$$\begin{aligned} &f(n_1, n_2, N, x_1, x_2) = f_*(n_1 + n_2, N, x_1) \\ &\quad + (x_1 - x_2)n_2\big(\xi(n_1 + n_2, N, x_1) + (x_1 - x_2)\rho(n_1, n_2, N, x_1, x_2)\big) \end{aligned} \tag{2.2.24}$$

for any $(n_1, n_2, N, x_1, x_2) \in \mathcal{U}_2$.

A generalized version of this theorem in the case of $\mathcal{U}_k$ will be proven in Appendix A.2.

Proof of Proposition 2.2.11. Set

$$\begin{aligned} f_1(n_1, N, x_1) &= 1 - (n_1 + n_2), \\ q_1(n_1, N, x_1) &= N(1 - N), \\ q_2(n_1, n_2, N, x_1, x_2) &= N(1 - N). \end{aligned}$$

Then $((f_1, q_1), (f, q_2))$ is a (2HS).
(1) Set $\varphi(n_1, n_2) = \alpha(n_1)^2 + \beta n_1 n_2 + \gamma(n_2)^2$ and define

$$\begin{aligned} G(n_1, n_2, N, x_1, x_2, y) = 1 - (n_1 + n_2) &+ (x_2 - y)n_2\varphi(n_1, n_2) \\ &+ (x_1 - y)n_1\varphi(n_2, n_1). \end{aligned}$$

Then $G(n_1, n_2, N, x_1, x_2, x_1) = f(n_1, n_2, N, x_1, x_2)$. Moreover (G1) and (G3) hold. Furthermore, (G2) holds if and only if $n_2\varphi(n_1, n_2) + n_1\varphi(n_2, n_1)$ only depends on $n_1 + n_2$. A routine calculation shows that this is equivalent to the condition that $\beta + \gamma = 3\alpha$.
(2) Comparing (2.2.23) and (2.2.24), we see that f is a part of (3HS) if and only if $\varphi(n_1, n_2)$ depends only on $n_1 + n_2$. This turns out to be equivalent to the condition that $\alpha = \gamma$ and $\beta = 2\alpha$. $\square$

2.2.3 Example

In this subsection, we give a class of examples which is simple enough as the fitness function f_2 is a polynomial of degree 2 in n_1 and n_2 but is out of the scope of the preceding framework by Dercole and Rinaldi. Indeed, we do show in Proposition 2.2.13 that no generating function is associated with it except the case where $a = b$ in the following example. Still we can show the occurrence of SU-shift and US-shift due to Theorem 2.2.3. As a reminder, our example is (2.1.8) given by

$$\begin{aligned} \frac{dn_1}{dt} &= n_1\big(1 - (n_1 + n_2) + (x_2 - x_1)n_2(c - an_1 - bn_2)\big) \\ \frac{dn_2}{dt} &= n_2\big(1 - (n_1 + n_2) + (x_1 - x_2)n_1(c - an_2 - bn_1)\big) \\ \frac{dN}{dt} &= N(1 - N), \end{aligned}$$

where a, b and c are real-valued parameters. In this case, if

$$\begin{aligned} f_2(n_1, n_2, N, x_1, x_2) &= 1 - (n_1 + n_2) + (x_2 - x_1)n_2(c - an_1 - bn_2), \\ q_2(n_1, n_2, N, x_1, x_2) &= N(1 - N), \\ f_1(n_1, N, x_1) &= 1 - n_1 \\ q_1(n_1, N, x_1) &= N(1 - N), \end{aligned}$$

then $(f_1, q_1), (f_2, q_2)$ is a (2HS) corresponding (2.1.8).

Proposition 2.2.13. *f_2 has an associated generating function if and only if $a = b$*

Proof. It follows that

$$\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_2) = b(n_1)^2 + 2an_1n_2 + b(n_2)^2 - c(n_1 + n_2). \quad (2.2.25)$$

By Theorem 2.2.10, the desired conclusion is immediate. □

The following theorem gives us variety of asymptotic behaviors of solutions of (2.1.8) according to the values of parameters a, b and c. In particular, it tells us that invasion does not always imply substitution.

Theorem 2.2.14. *Let $x_* \in \mathbb{R}$. Then*
(1) *If $b - c > 0$ and $a + b - 2c > 0$, then SU-shift occurs at x_*.*
(2) *If $b - c < 0$ and $a + b - 2c < 0$, then US-shift occurs at x_*.*

(3) *Suppose that* $(b-c)(a+b-2c) < 0$. *Then two distinct locally stable equilibrium coexist if* $x_2 \neq x_*$ *and* $|x_2 - x_*|$ *is sufficiently small. More precisely, assume* $b > c$ *(resp.* $b < c$.*) Then there exists* $\delta > 0$ *and* ϵ *such that the following two cases occur.*
(3A) $x_2 \in (x_*, x_*+\delta)$ *(resp.* $(x_*-\delta, x_*)$*): There exists a locally stable equilibrium point* $(\widetilde{n}_{x_*}, \widetilde{n}_{x_2}, 1)$ *such that any solution starting from* $B((1,0,1),\epsilon) \cap (0,\infty)^3$ *converges to* $(\widetilde{n}_{x_*}, \widetilde{n}_{x_2}, 1)$*as* $t \to \infty$. *The mutant dominant equilibrium point* $(0,1,1)$ *is also locally stable.*
(3B) $x_2 \in (x_* - \delta, x_*)$ *(resp.* $(x_*, x_* + \delta)$*): The resident dominant equilibrium* $(1,0,1)$ *is locally stable. There exists a locally stable equilibrium point* $(\overline{n}_{x_*}, \overline{n}_{x_2}, 1)$ *such that any solution starting from* $B((0,1,1),\epsilon) \cap (0,\infty)^3$ *converges to* $(\overline{n}_{x_*}, \overline{n}_{x_2}, 1)$*as* $t \to \infty$.

Proof. For (1) and (2), making use of (2.2.23), we verify (2.2.2) and (2.2.3) in Theorem 2.2.3 respectively. The proof of (3) is in A.4 □

As we have already mentioned in the introduction, the case (3) of the above theorem reveals a phenomenon beyond IIS principle. There exist two locally stable equilibria. In the case of (3A), if the initial population of mutants is relatively small, then residents and mutants will coexist in a certain proportion. If the initial population of mutants is large enough mutants will dominate the entire population eventually, although this may not sound realistic in the real world. In summary, the final outcome of the competition really depends on the initial configuration right after a mutation.

Appendix A

Proofs

A.1 Proof of Theorem 2.2.3

In this appendix, we are going to prove Theorem 2.2.3. As a reminder, our system is a (2HS), i.e. (DMS) and (MMS) satisfying Assumption 2.2.1 and the consistency conditions (2.1.2) and (2.1.3). We fix $x_* \in \mathbb{R}$ throughout this section. If no confusion may occur, an element of $\mathbb{R}^2$ is thought of as either a row vector (a_1, a_2) or a column vector $\begin{pmatrix} a_1 \\ a_2 \end{pmatrix}$ from place to place for convenience hereafter in this paper. For simplicity, we define vector fields V_1 on $\mathcal{U}_1$ and V_2 on $\mathcal{U}_2$ as follows:

$$V_1(n_1, N, x_*) := \begin{pmatrix} n_1 f_1(n_1, N, x_*) \\ q_1(n_1, N, x_*) \end{pmatrix}$$

$$V_2(n_1, n_2, N, x_*, x_2) := \begin{pmatrix} n_1 f_2(n_1, n_2, N, x_*, x_2) \\ n_2 f_2(n_2, n_1, N, x_2, x_*) \\ q_2(n_1, n_2, N, x_*, x_2) \end{pmatrix}$$

Lemma A.1.1. *Set $v_* = (\widehat{n}_*, \widehat{N}_*)$. There exist a positive definite quadratic form $p : \mathbb{R}^2 \to \mathbb{R}_+$, $\epsilon_0 > 0$ and $a > 0$ such that, if $v \in B_{\epsilon_0}(v_*)$, then*

$$\langle \nabla p(v - v_*), V_1(n_1, N, x_*) \rangle \leq -a \left\| v - v_* \right\|^2 \tag{1.1.1}$$

where

$$\nabla f = \begin{pmatrix} \dfrac{\partial f}{\partial s_1} \\ \dfrac{\partial f}{\partial s_2} \end{pmatrix}$$

for a smooth function $f(s_1, s_2)$ and $\|\cdot\|$ is the standard Euclidean norm of $\mathbb{R}^2$.

Proof. Without loss of generality, we may assume that $v_* = (0,0)$. Let J_1 be the Jacobi matrix of vector field V_1 at v_*. Let P be a 2×2 real regular matrix transforming J_1 into the real Jordan normal form, i.e. PJ_1P^{-1} is the real Jordan normal form of J_1. According to the Jordan normal form of J_1, we have three cases. Namely, $PJ_1P^{-1} = A_1$ or A_2 or A_3, where

$$A_1 = \begin{pmatrix} t_1 & 0 \\ 0 & t_2 \end{pmatrix}, A_2 = \begin{pmatrix} \alpha & 1 \\ 0 & \alpha \end{pmatrix} \text{ and } A_3 = \begin{pmatrix} \alpha & -\beta \\ \beta & \alpha \end{pmatrix}$$

with $t_1, t_2, \alpha < 0$ and $\beta \in \mathbb{R}$. For convenience of notation, we write $A = PJ_1P^{-1}$.

Set $\tilde{p}_c(s_1, s_2) := {s_1}^2 + c{s_2}^2$, where the constant $c > 0$ will be determined eventually in accordance with our purpose.

Claim 1: There exist $c > 0$ and $a' > 0$ such that

$$\langle \nabla \tilde{p}_c(u), Au \rangle \leq -a' \|u\|^2, \tag{1.1.2}$$

for any $u \in \mathbb{R}^2$.

Proof of Claim 1: Suppose $A = A_2$. Then

$$(\nabla \tilde{p}_c(u), A_2 u) = 2(\alpha {u_1}^2 + u_1 u_2 + c\alpha u_2^2)$$

for any $u = (u_1, u_2) \in \mathbb{R}^2$. Since $\alpha < 0$, it follows that the right-hand of the above equality is negative definite if $c > 1/4\alpha^2$. Therefore, we have verified Claim 1 in this case. Similar argument works for the rest of the cases as well. □

Since P is an invertible matrix, there exists $a'' > 0$ such that

$$-a' \|Pu\|^2 \leq -a'' \|u\|^2$$

for any $u \in \mathbb{R}^2$. Set $p_c(u) = \tilde{p}_c(Pu)$. Then

$$\nabla p_c(u) = {}^tP \nabla \tilde{p}_c(Pu),$$

where ${}^tP$ is the transpose of P. Now, since

$$V_1(v, x_*) = J_1 v + O(\|v\|^2)$$

as $\|v\| \to 0$, we verify that

$$(\nabla p_c(v), V_1(v, x_*)) = (\nabla \tilde{p}_c(Pv), APv) + O(\|v\|^3) \tag{1.1.3}$$

as $\|v\| \to 0$. At the same time, by Claim 1, it follows that

$$(\nabla \tilde{p}_c(Pv), APv) \leq -a' \|Pv\|^2 \leq -a'' \|v\|^2 \tag{1.1.4}$$

for any $v \in \mathbb{R}^2$. Combining (1.1.3) and (1.1.4), we see that there exist $\epsilon_0 > 0$ and $a > 0$ such that

$$(\nabla p_c(v), V_1(v, x_*)) \leq -a \|v\|^2$$

for any $v \in B_{\epsilon_0}(v_*)$. $\square$

Let p be the positive definite quadratic form obtained in Lemma A.1.1. For $r > 0$, we define a r-Tube T_r by

$$T_r = \left\{ (n_1, n_2, N) \in (\mathbb{R}_+)^2 \times \mathbb{R} \;\middle|\; p(n_1 + n_2 - \widehat{n}_{x_*}, N - \widehat{N}_{x_*}) \leq r^2 \right\}.$$

Note that T_r is a tubular neighborhood of

$$\{(n_1, n_2, N) \mid (n_1, n_2, N, x_*, x_*) \in L(x_*)\}.$$

We call a domain $U \subseteq \mathcal{U}_2$ is *invariant* if every solution $(n_1(t), n_2(t), N(t))$ of (DMS1) starting from U stays in U for any $t > 0$.

Lemma A.1.2. *There exists $\epsilon_1 > 0$ such that, for any $\epsilon < \epsilon_1$, one may choose $\delta > 0$ so that T_ϵ is invariant if $|x_* - x_2| < \delta$.*

Remark A.1.1. *This lemma corresponds to the tube theorem in [14].*

Proof. Let ϵ_0 be the constant obtained in Lemma A.1.1. Then, there exists $\epsilon_1 > 0$ such that

$$T_{\epsilon_1} \subseteq \{(n_1, n_2, N) \mid (n_1 + n_2, N) \in B_{\epsilon_0}(v_*)\}.$$

Let $(n_1, n_2, N) \in T_{\epsilon_1}$ and let $v(t) = (n_1(t), n_2(t), N(t))$ be the solution of (DMS1) satisfying $(n_1(0), n_2(0), N(0)) = (n_1, n_2, N)$. Then

$$\frac{d}{dt} p(v(t) - v_*)|_{t=0} = 2(\nabla p(v - v_*), \widetilde{V}), \tag{1.1.5}$$

where

$$\widetilde{V} = \begin{pmatrix} n_1 f_2(n_1, n_2, N, x_*, x_2) + n_2 f_2(n_2, n_1, N, x_2, x_*) \\ q_2(n_1, n_2, N, x_*, x_2) \end{pmatrix}$$

In case $x_2 = x_*$, since $\widetilde{V} = V_1(n_1 + n_2, N, x_*)$, Lemma A.1.1 yields

$$\begin{aligned} \frac{d}{dt} p(v(t) - v_*)|_{t=0} &= 2(\nabla p(v - v_*), V_1(n_1 + n_2, N, x_*)) \\ &\leq -2a \|v - v_*\|^2, \end{aligned} \tag{1.1.6}$$

where $v = (n_1 + n_2, N)$. Set

$$\partial_1 T_\epsilon = \left\{ (n_1, n_2, N) \;\middle|\; p(v - v_*) = \epsilon^2, n_1, n_2 \geq 0 \right\}.$$

Since $\partial_1 T_\epsilon$ is compact, by (1.1.6), there exists $M > 0$ such that

$$\begin{aligned} \frac{d}{dt} p(n_1(t) + n_2(t), N(t))|_{t=0} = (\nabla p(v - v_*), V_1(n_1 + n_2, N, x_1)) \\ \leq -M \end{aligned}$$

for any $(n_1, n_2, N) \in \partial_1 T_\epsilon$. As $\widetilde{V}$ is continuous on the compact set

$$\partial_1 T_\epsilon \times \{x_*\} \times [x_* - \delta, x_* + \delta],$$

if $\delta > 0$ is sufficiently small, then

$$\frac{d}{dt} p(v(t) - v_*)|_{t=0} = 2(\nabla p(v - v_*), \widetilde{V}) \leq -\frac{M}{2} \tag{1.1.7}$$

for any $(n_1, n_2, N, x_*, x_2) \in \partial_1 T_\epsilon \times \{x_*\} \times [x_* - \delta, x_* + \delta]$. This means that the solution $v(t)$ can not escape T_ϵ through $\partial_1 T_\epsilon$.

The rest of the boundary ∂T_ϵ of T_ϵ as a subset of $\mathbb{R}^3$ is included in two planes

$$\{(n_1, n_2, N) \mid n_1, n_2 \geq 0, n_1 = 0 \text{ or } n_2 = 0\}.$$

Hence one easily see that the solution $v(t)$ can not escape T_ϵ through this part as well. Thus T_ϵ is invariant if $|x_* - x_2| \leq \delta$.

□

Now, let us complete the proof of Theorem 2.2.3.

Proof of Theorem 2.2.3. Let p and T_r be the same as before. Assume that there exists $c > 0$ such that

$$\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_2) > c$$

for any $(n_1, n_2, N, x_1, x_2) \in L(x_*)$. Since $\frac{\partial \Theta}{\partial x_2}$ is continuous on the compact set $T_\epsilon \times \{x_*\} \times [x_* - \epsilon, x_* + \epsilon]$, if $\epsilon > 0$ is sufficiently small, then

$$\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_2) > c/2$$

for any $(n_1, n_2, N, x_1, x_2) \in T_\epsilon \times \{x_*\} \times [x_* - \epsilon, x_* + \epsilon]$. In addition, we let $0 < \epsilon < \epsilon_1$, where ϵ_1 is the constant appearing in Lemma A.1.2. Furthermore

choose $\delta_0 > 0$ so that $\delta_0 \le \min\{\epsilon, \delta\}$, where δ is the constant appearing in Lemma A.1.2. Consequently, what we have shown so far is
(1) T_ϵ is invariant if $|x_* - x_2| \le \delta_0$.
(2) For any $(n_1, n_2, N, x_1, x_2) \in T_\epsilon \times \{x_*\} \times [x_* - \delta_0, x_* + \delta_0]$,

$$\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_2) > c/2.$$

We assume that $|x_* - x_2| \le \delta_0$ hereafter in this proof. By elementary calculation, if $R(t) = n_1(t)/(n_1(t) + n_2(t))$ for a solution $(n_1(t), n_2(t), N(t))$ of (DMS1) starting from an interior point of T_ϵ, then

$$\begin{aligned}\frac{dR}{dt} &= -R(1-R)\Theta(n_1, n_2, N, x_*, x_2)\\ &= -R(1-R)(x_2 - x_*)\int_0^1 \frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_*, (1-s)x_* + sx_2)ds. \quad (1.1.8)\end{aligned}$$

Assume $x_2 \in (x_*, x_* + \delta_0)$. As T_ϵ is invariant, $(n_1(t), n_2(t), N(t))$ stays in T_ϵ for any $t > 0$. Moreover by (2), it follows that

$$\frac{dR}{dt} \le -\frac{c}{2}(x_2 - x_*)R(1-R).$$

for any $t > 0$. Thus $R(t) \to 0$ as $t \to \infty$ and hence $n_1(t) \to 0$ as $t \to \infty$.

Set $\mathcal{U}_{21} = \{(n_1, n_2, N) | (n_1, n_2, N) \in \mathcal{U}_2, n_1 = 0\}$ and $D_2 = T_\epsilon \cap \mathcal{U}_{21}$

Claim 1: The fixed point $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ belongs to D_2.

Proof of Claim 1: As both T_ϵ and $\mathcal{U}_{21}$ are invariant, we see that D_2 is invariant. Moreover, the system (DMS1) is (MMS) with the parameter x_2 on $\mathcal{U}_{21}$ and this system restricted on $\mathcal{U}_{21}$ has the unique attractive fixed point $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$. Considering that D_2 is invariant, we conclude that the fixed point $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ belongs to D_2. □

Claim 2: The fixed point $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ is attractive.

Proof of Claim 2: Direct calculation shows that the linearization of (DMS) at $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ is given by

$$\begin{pmatrix} f_2(0, \widehat{n}_{x_2}, \widehat{N}_{x_2}, x_*, x_2) & 0 & 0 \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

where $\begin{pmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{pmatrix}$ equals (2.2.1) with $x = x_2$ whose eigenvalues have negative real parts by Assumption 2.2.1. The remaining eigenvalue is

$$f_2(0, \widehat{n}_{x_2}, \widehat{N}_{x_2}, x_*, x_2) = -\Theta(0, \widehat{n}_{x_2}, \widehat{N}_{x_2}, x_*, x_2).$$

Since $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2}, x_*, x_2) \in T_\epsilon$, the same argument as in (1.1.8) implies that $\Theta(0, \widehat{n}_{x_2}, \widehat{N}_{x_2}, x_*, x_2) > 0$. $\square$

Now since $n_1(t) \to 0$ as $t \to \infty$, if $u_* \in \mathcal{U}_2$ is an ω-limit set of the orbit $(n_1(t), n_2(t), N(t))$, then $\omega \in D_2$. In other words, there exists a sequence $\{t_m\}_{m\geq 1}$ such that $0 < t_1 < t_2 < \ldots$ and $(n_1(t_m), n_2(t_m), N(t_m)) \to u_* \in D_2$ as $m \to \infty$. Now let $u(t)$ be the solution of (DMS1) staring from $u_* \in D_2$. As D_2 is invariant and $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ is an attractor on D_2, $u(t) \to (0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ as $t \to \infty$. Note that $(n_1(t_m+s), n_2(t_m+s), N(t_m+s)) \to u(s)$ as $m \to \infty$. This implies that $(n_1(t), n_2(t), N(t))$ will eventually enter the basin of attraction of $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$. Therefore, we conclude that any solution $(n_1(t), n_2(t), N(t))$ of (DMS1) starting from the interior of T_ϵ is convergent to $(0, \widehat{n}_{x_2}, \widehat{N}_{x_2})$ as $t \to \infty$.

Through similar discussion, it is shown that if $x_2 \in [x_* - \delta_0, x_*)$, then any solution $(n_1(t), n_2(t), N(t))$ of (DMS1) starting from the interior of T_ϵ is convergent to $(0, \widehat{n}_{x_*}, \widehat{N}_{x_*})$ as $t \to \infty$. Since $S_{\epsilon'}(x_*) \subseteq T_\epsilon$ for sufficiently small $\epsilon' > 0$, we have shown that SU-shift occurs in this case.

Analogous arguments yield the occurrence of US-shift if there exists $c > 0$ such that

$$\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_2) < -c$$

for any $(n_1, n_2, N, x_1, x_2) \in L(x_*)$. $\square$

A.2 Proof of Proposition 2.2.12

In this section, we are going to prove Proposition 2.2.12. Let

$$\mathcal{U}_k = (\mathbb{R}_+)^k \times \mathbb{R} \times \mathbb{R}^k$$

and define $C^\infty(\mathcal{U}_k)$ as the collection of functions on $\mathcal{U}_k$ which are C^∞ on neighborhoods of $\mathcal{U}_k$; more precisely,

$$C^\infty(\mathcal{U}_k) = \left\{ u : \mathcal{U}_k \to \mathbb{R} \;\middle|\; \begin{array}{l} \text{there exist an open set } \mathcal{U} \supseteq \mathcal{U}_k \text{ and a } C^\infty\text{-} \\ \text{function } \widetilde{u} : \mathcal{U} \to \mathbb{R} \text{ such that } \widetilde{u}|_{\mathcal{U}_k} = u. \end{array} \right\}$$

To define the explicit notion of symmetry, we introduce the k-dimensional permutation group $\mathfrak{S}_k$ as

$$\mathfrak{S}_k = \{\sigma : \{1, \ldots, k\} \to \{1, \ldots, k\} \mid \sigma \text{ is bijective.}\}$$

For $\sigma \in \mathfrak{S}_k$, we define $\iota_\sigma : \mathcal{U}_k \to \mathcal{U}_k$ by

$$\iota_\sigma(n, N, x) = (n_{\sigma^{-1}(1)}, \ldots, n_{\sigma^{-1}(k)}, N, x_{\sigma^{-1}(1)}, \ldots, x_{\sigma^{-1}(k)}),$$

where $n = (n_1, \ldots, n_k)$ and $x = (x_1, \ldots, x_k)$.
Let $i \in \{1, \ldots, k\}$. Define $d_i^k : \mathcal{U}_k \to \mathcal{U}_{k-1}$ by

$$d_i^k(n, N, x) = (n_1, \ldots, n_{i-1}, n_{i+1}, \ldots, n_k, N, x_1, \ldots, x_{i-1}, x_{i+1}, \ldots, x_k).$$

Let $1 \leq i < j \leq k$. Define $d_{i,j}^k : \mathcal{U}_k \to \mathcal{U}_{k-1}$ by

$$d_{i,j}^k(n, N, x) = d_j^k(n_1, \ldots, n_{i-1}, n_i + n_j, n_{i+1}, \ldots, n_{j-1}, n_{j+1}, \ldots, n_k, N, x)$$

for any $n = (n_1, \ldots, n_k)$, N and $x = (x_1, \ldots, x_k)$

Definition A.2.1. *A function $f : \mathcal{U}_k \to \mathbb{R}$ is said to have $\mathfrak{S}_{k-1}$-symmetry if and only if*

$$f(n, N, x) = f(\iota_\sigma(n, N, x))$$

for any $n = (n_1, \ldots, n_k)$, $N \in \mathbb{R}$ and $x = (x_1, \ldots, x_k)$ whenever $\sigma \in \mathfrak{S}_k$ and $\sigma(1) = 1$.

The above condition of having $\mathfrak{S}_{k-1}$-symmetry is the generalization of the symmetry condition (2.2.8) to arbitrary number of strategies.

Next we give definitions corresponding to the properties (ET) and (CT) in the definition of trimorphic systems in Definition 2.2.5.

Definition A.2.2. *Let $j \in \mathbb{N}$.*
(1) Let $2 \leq i \leq j$. A pair $(f_j, f_{j-1}) \in C^\infty(\mathcal{U}_j) \times C^\infty(\mathcal{U}_{j-1})$ is said to satisfy the property $(\mathrm{ET})_i^j$ if and only if

$$f_j(n, N, x) = f_{j-1}(d_i^j(n, N, x)),$$

where $n = (n_1, \ldots, n_j)$, $N \in \mathbb{R}$ and $x = (x_1, \ldots, x_j)$, provided $n_i = 0$.
(2) Let $1 \leq i < j \leq n$ and $x_i = x_j$. A pair $(f_j, f_{j-1}) \in C^\infty(\mathcal{U}_j) \times C^\infty(\mathcal{U}_{j-1})$ is said to satisfy the property $(\mathrm{CT})_{i,m}^j$ if and only if

$$f_j(n, N, x) = f_{j-1}(d_{i,m}^j(n, N, x)),$$

where $n = (n_1, \ldots, n_j)$, $N \in \mathbb{R}$ and $x = (x_1, \ldots, x_j)$, provided $x_i = x_m$.

The expressions (ET) and (CT) in the above definition represent "Extinction of a Trait value" and "Coincidence of Trait values" respectively. For example, the properties $(\mathrm{ET})_3^3$, $(\mathrm{CT})_{1,2}^3$, $(\mathrm{CT})_{2,3}^3$ correspond to (2.2.10), (2.2.12) and (2.2.13) respectively. Moreover, the properties $(\mathrm{ET})_2^2$ and $(\mathrm{CT})_{1,2}^2$

correspond to (2.1.2) and (2.1.3) respectively. In fact, if we study systems of ODE's representing general multi-morphic system

$$\begin{aligned}
\frac{dn_1}{dt} &= n_1 f_k(n_1, n_2, \dots, n_k, N, x_1, x_2, \dots, x_k)\\
&\vdots\\
\frac{dn_k}{dt} &= n_1 f_k(n_k, n_1, \dots, n_{k-1}, N, x_m, x_1, \dots, x_{k-1})\\
\frac{dN}{dt} &= q_k(n_1, \dots, n_k, N, x_1, \dots, x_k)
\end{aligned}$$

for $k = 1, \dots, m$, the natural condition for the consistency of the systems with different values of k is that, for any $k = 2, \dots, m$, f_k has $\mathfrak{S}_{k-1}$-symmetry and (f_k, f_{k-1}) satisfy $(\mathrm{ET})_i^k$ for $i = 2, \dots, k$ and $(\mathrm{CT})_{i,j}^k$ for any $1 \le i < j \le k$. In such a case, the sequence $((f_i, q_i))_{i=1,\dots,k}$ should be called a k-hierarchical system, (kHS) for short, as a natural extension of the notions of (2HS) and (3HS).

Under a weaker set of properties, the functions $f_1, \dots, f_m$ are shown to have special forms in the next lemma.

Lemma A.2.3. *Let $m \ge 1$. For $(f_1, \dots, f_m) \in C^\infty(\mathcal{U}_1) \times \dots \times C^\infty(\mathcal{U}_m)$, the following conditions* (a) *and* (b) *are equivalent:*
(a) *For each $k \in \{2, \dots, m\}$, f_k has $\mathfrak{S}_{k-1}$-symmetry and the pair (f_k, f_{k-1}) satisfies* $(\mathrm{ET})_i^k$ *and* $(\mathrm{CT})_{1,i}^k$ *for any $i = 2, 3, \dots, k$.*
(b) *There exists a sequence $\{h_k\}_{k=1,\dots,m}$ such that for any $k = 1, \dots, m$, $h_k \in C^\infty(\mathcal{U}_k)$ and for any $k = 2, \dots, m$, h_k has $\mathfrak{S}_{k-1}$-symmetry and*

$$f_k(n, N, x) = \sum_{j=0}^{k-1} \sum_{2 \le i_1 < \dots < i_j \le k} \left(\prod_{l=1}^{j} n_{i_l}(x_1 - x_{i_l}) \right) h_{j+1,k}^{(i_1,\dots,i_j)}(n, N, x) \quad (1.2.1)$$

for any $(n, N, x) \in \mathcal{U}_k$, where $n = (n_1, \dots, n_k)$, $x = (x_1, \dots, x_k)$ and

$$h_{j+1,k}^{(i_1,\dots,i_j)}(n, N, x) = h_{j+1}\Big(\sum_{i=1}^{k} n_i - \sum_{l=1}^{j} n_{i_l}, n_{i_1}, \dots, n_{i_j}, N, x_1, x_{i_1}, \dots, x_{i_j} \Big).$$

Note that in the above lemma, the property $(\mathrm{CT})_{i,j}^k$ is assumed only if $i = 1$.

For $k = 2, 3$, (1.2.1) can be written as

$$f_2(n_1, n_2, N, x_1, x_2) = f_1(n_1 + n_2, N, x_1) + n_2(x_1 - x_2) h_2(n_1, n_2, N, x_1, x_2) \quad (1.2.2)$$

and

$$f_3(n_1,n_2,n_3,N,x_1,x_2,x_3) = f_1(n_1+n_2+n_3,N,x_1)+ \\ n_2(x_1-x_2)h_2(n_1+n_3,n_2,N,x_1,x_2)+n_3(x_1-x_3)h_2(n_1+n_2,n_3,N,x_1,x_3)+ \\ n_2n_3(x_1-x_2)(x_1-x_3)h_3(n_1,n_2,n_3,N,x_1,x_2,x_3). \quad (1.2.3)$$

Proof. For the sake of simplicity of the expression, we omit to write the variable N explicitly in this proof.

We use an induction on m. If $m=1$, it is obvious.

Let $m \geq 2$. Assume that the statement holds for $1,\ldots,m-1$. Define $\psi_m : \mathcal{U}_m \to \mathbb{R}$ by

$$\psi_m(n,x) = \sum_{j=0}^{m-2} \sum_{2\leq i_1<\ldots<i_j\leq m} \left(\prod_{l=1}^{j} n_{i_l}(x_1-x_{i_l})\right) h_{j+1,m}^{(i_1,\ldots,i_j)}(n,x),$$

where $n=(n_1,\ldots,n_m)$ and $x=(x_1,\ldots,x_m)$.

Assume $n_i=0$ for some $i\geq 2$. Set $(\tilde{n},\tilde{x}) = d_i^m(n,x)$. Then by $(\mathrm{ET})_i^m$, we have

$$f_m(n,x) = f_{m-1}(\tilde{n},\tilde{x}),$$

On the other hand, since $n_i=0$, we see that

$$\psi_m(n,x) = \sum_{j=0}^{m-2} \sum_{2\leq i_1<\ldots<i_j\leq m-1} \left(\prod_{l=1}^{j} \tilde{n}_{i_l}(\tilde{x}_1-\tilde{x}_{i_l})\right) h_{j+1,m-1}^{(i_1,\ldots,i_j)}(\tilde{n},\tilde{x}).$$

Note that (1.2.1) holds for $k=m-1$ by the induction hypothesis. Hence the right-hand side of the above equality coincides with $f_{m-1}(\tilde{n},\tilde{x})$. Therefore it follows that

$$f_m(n,x)-\psi_m(n,x)=0$$

if $n_i=0$ for some $i\geq 2$.

Next assume that $x_i=x_1$ for some $i\geq 2$. Let $(\hat{n},\hat{x}) = d_{1,i}^m(n,x)$. Then by $(\mathrm{CT})_{1,i}^m$,

$$f_m(n,x) = f_{m-1}(\hat{n},\hat{x}).$$

At the same time, since $x_1-x_i=0$, we see that

$$\psi_m(n,x) = \sum_{j=0}^{m-2} \sum_{2\leq i_1<\ldots<i_j\leq m-1} \left(\prod_{l=1}^{j} \hat{n}_{i_l}(\hat{x}_1-\hat{x}_{i_l})\right) h_{j+1,m-1}^{(i_1,\ldots,i_j)}(\hat{n},\hat{x}).$$

Note that (1.2.1) holds for $k = m-1$ by the induction hypothesis. Hence the right-hand side of the above equality coincides with $f_{m-1}(\hat{n}, \hat{x})$. Thus we have shown that

$$\psi_m(n, x) = f_{m-1}(\hat{n}, \hat{x}).$$

Hence if $x_1 - x_i = 0$ for some $i \geq 2$, then

$$f_m(n, x) - \psi_m(n, x) = 0$$

Thus it follows that $f_m(n, x) - \psi_m(n, x)$ can be divided by $\prod_{i=2}^{m} n_i(x_1 - x_i)$. Therefore, there exists $h_m : \mathcal{U}_m \to \mathbb{R}$ such that h_m has $\mathfrak{S}_{m-1}$-symmetry and

$$f_m(n, x) - \psi_m(n, x) = \prod_{i=2}^{m} n_i(x_1 - x_i) h_m(n, x).$$

Thus the desired statement is true for m. □

As a corollary of Lemma A.2.3, we have the following lemma.

Lemma A.2.4. *$f \in C^\infty(\mathcal{U}_2)$ is a part of (2HS) if and only if there exist $f_* \in C^\infty(\mathcal{U}_1)$ and $\varphi \in C^\infty(\mathcal{U}_2)$ such that*

$$f(n_1, n_2, N, x_1, x_2) = f_*(n_1+n_2, x_1) + n_2(x_2 - x_1)\varphi(n_1, n_2, N, x_1, x_2) \quad (1.2.4)$$

for any $(n_1, n_2, N, x_1, x_2) \in \mathcal{U}_2$.

Proof. Assume that f is a part of (2HS). Let $((f_1, q_1), (f_2, q_2))$ be a (2HS) satisfying $f = f_2$. Then the condition (a) in Lemma A.2.3 holds for (f_2, f_1). Hence we obtain (1.2.4) from (1.2.2). Conversely suppose that (1.2.4) holds. Define $f_2 = f, f_1 = f_*, q_1 \equiv 0$ and $q_2 \equiv 0$. Then $((f_1, q_1), (f_2, q_2)$ is a (2HS) and f is a part of (2HS). □

Assuming the full properties of $(\mathrm{ET})_i^k$ and $(\mathrm{CT})_{i,j}^k$ for $k = 2, 3$, we obtain the following theorem, which includes the restatement of Proposition 2.2.12. In fact, (1.2.5) is exactly (2.2.24).

Theorem A.2.5. *Let $(f_1, f_2, f_3) \in C^\infty(\mathcal{U}_1) \times C^\infty(\mathcal{U}_2) \times C^\infty(\mathcal{U}_3)$. The following conditions* (c) *and* (d) *are equivalent.*
(c) *For $k = 2, 3$, f_k is $\mathfrak{S}_{k-1}$-symmetric and the pair (f_k, f_{k-1}) satisfies* $(\mathrm{ED})_i^k$ *for any $2 \leq i \leq k$ and* $(\mathrm{CT})_{i,j}^k$ *for any $1 \leq i < j \leq k$.*
(d) *There exist $\xi \in C^\infty(\mathcal{U}_1)$, $\rho \in C^\infty(\mathcal{U}_2)$ and $F \in C^\infty(\mathcal{U}_3)$ such that, for any $(n_1, n_2, n_3, N, x_1, x_2, x_3) \in \mathcal{U}_3$,*

$$F(n_1, n_2, n_3, N, x_1, x_2, x_3) = -F(n_1, n_3, n_2, N, x_1, x_3, x_2),$$

$$
\begin{aligned}
&f_2(n_1, n_2, N, x_1, x_2) = f_1(n_1 + n_2, N, x_1) + \\
&\qquad n_2(x_1 - x_2)\big(\xi(n_1 + n_2, N, x_1) + (x_1 - x_2)\rho(n_1, n_2, N, x_1, x_2)\big) \quad (1.2.5)
\end{aligned}
$$

and

$$
\begin{aligned}
&f_3(n, N, x) = f_1(n_1 + n_2 + n_3, N, x_1) + \\
&\qquad \big(n_2(x_1 - x_2) + n_3(x_1 - x_3))\xi(n_1 + n_2 + n_3, N, x_1)\big) + \\
&\qquad n_2(x_1 - x_2)(x_3 - x_2)\rho(n_1 + n_3, n_2, N, x_1, x_2) + \\
&\qquad n_3(x_1 - x_3)(x_2 - x_3)\rho(n_1 + n_2, n_3, N, x_1, x_3) + \\
&(x_1 - x_2)(x_1 - x_3)\big(n_2\rho(n_1, n_2 + n_3, N, x_1, x_2) + n_3\rho(n_1, n_2 + n_3, N, x_1, x_3)\big) + \\
&\qquad n_2 n_3(x_1 - x_2)(x_1 - x_3)(x_2 - x_3)F(n, N, x),
\end{aligned}
$$

where $n = (n_1, n_2, n_3)$ *and* $x = (x_1, x_2, x_3)$.

Proof. As we have done in the proof of Lemma A.2.3, we omit to write N explicitly in the followings.
(c) $\Rightarrow$ (d): By Lemma A.2.3, we have (1.2.2) and (1.2.3). Let $x_2 = x_3$ in (1.2.3). By $(\mathrm{CT})^3_{2,3}$, we have

$$
\begin{aligned}
&n_2 h_2(n_1 + n_3, n_2, x_1, x_2) + n_3 h_2(n_1 + n_2, n_3, x_1, x_2) \\
&\qquad + n_2 n_3(x_1 - x_2)h_3(n, x) = (n_2 + n_3)h_2(n_1, n_2 + n_3, x_1, x_2). \quad (1.2.6)
\end{aligned}
$$

Define $H(X, Y, x_1) = Yh_2(X - Y, Y, x_1, x_1)$. Then by (1.2.6), we obtain

$$
\begin{aligned}
&H(n_1 + n_2 + n_3, n_2, x_1) + H(n_1 + n_2 + n_3, n_3, x_1) \\
&\qquad = H(n_1 + n_2 + n_3, n_2 + n_3, x_1).
\end{aligned}
$$

This implies

$$
H(t, s_1, x_1) + H(t, s_2, x_1) = H(t, s_1 + s_2, x_1)
$$

for any $t, s_1, s_2 \geq 0$ with $s_1 + s_2 \leq t$. Since H is C^∞, there exists $\xi \in C^\infty(\mathcal{U}_1)$ such that $H(t, s, x_1) = \xi(t, x_1)s$ if $0 \leq s \leq t$. Recalling the definition of H, we have

$$
h_2(n_1, n_2, x_1, x_1) = \xi(n_1 + n_2, x_1).
$$

Since $h_2(n_1, n_2, x_1, x_2) - h_2(n_1, n_2, x_1, x_1) \equiv 0$ if $x_1 = x_2$, there exists $\rho \in C^\infty(\mathcal{U}_2)$ such that

$$
h_2(n_1, n_2, x_1, x_2) = n_2\xi(n_1 + n_2, x_1) + (x_1 - x_2)\rho(n_1, n_2, x_1, x_2). \quad (1.2.7)
$$

This immediately yields (1.2.5). Next, define

$$\begin{aligned}\eta(n,x) = f_1(n_1+n_2+n_3,x_1)+&\\ \big(n_2(x_1-x_2)+n_3(x_1-x_3)\big)\xi(n_1+n_2+n_3,x_1)+&\\ n_2(x_1-x_2)(x_3-x_2)\rho(n_1+n_3,n_2,x_1,x_2)+&\\ n_3(x_1-x_3)(x_2-x_3)\rho(n_1+n_2,n_3.x_1,x_3)+&\\ (x_1-x_2)(x_1-x_3)\big(n_2\rho(n_1,n_2+n_3,x_1,x_2)+n_3\rho(n_1,n_2+n_3,x_1,x_3)\big).&\end{aligned}$$

Then, by (1.2.5),

$$\begin{aligned}&\eta(n_1,0,n_3,x_1,x_2,x_3) =\\ &f_1(n_1+n_3,x_1)+n_3(x_1-x_3)(\xi(n_1+n_3,x_1)+(x_1-x_3)\rho(n_1,n_3,x_1,x_3))\\ &\qquad = f_2(n_1,n_3,x_1,x_3).\end{aligned}$$

By $(\mathrm{ET})^3_2$, it follows that $\eta(n_1,0,n_3,x) = f_3(n_1,0,n_3,x)$. Similar arguments show that $\eta(n_1,n_2,0,x) = f_3(n_1,n_2,0,x)$. Moreover, by (1.2.5),

$$\begin{aligned}&\eta(n_1,n_2,n_3,x_1,x_1,x_3) = f_1(n_1+n_2+n_3,x_1)+\\ &\quad n_3(x_1-x_3)(\xi(n_1+n_2+n_3,x_1)+(x_1-x_3)\rho(n_1+n_2,n_3.x_1,x_3))\\ &\qquad = f_2(n_1+n_2,n_3,x_1,x_3).\end{aligned}$$

By $(\mathrm{CT})^3_{1,2}$, it follows that

$$\eta(n,x_1,x_1,x_3) = f_3(n,x_1,x_1,x_3).$$

In the same manner, using $(\mathrm{CT})^3_{1,3}$ and $(\mathrm{CT})^3_{2,3}$, we see that

$$\begin{aligned}\eta(n,x_1,x_2,x_1) &= f_3(n,x_1,x_2,x_3),\\ \eta(n,x_1,x_2,x_2) &= f_3(n,x_1,x_2,x_2).\end{aligned}$$

Thus, there exists $F \in C^\infty(\mathcal{U}_3)$ such that

$$f_3(n,x) - \eta(n,x) = n_2n_3(x_1-x_2)(x_1-x_3)(x_2-x_3)F(n,x).$$

Since f_3 has $\mathfrak{S}_2$-symmetry, it follows that

$$F(n_1,n_2,n_3,x_1,x_2,x_3) = -F(n_1,n_3,n_2,x_1,x_3,x_2).$$

(d) ⇒ (c): This is straightforward. □

A.3 Proof of Theorem 2.2.10

Throughout A.3, $((f_1, q_1), (f_2, q_2))$ is assumed to be a (2HS). There exists $\varphi \in C^\infty(\mathcal{U}_2)$, by Lemma A.2.4, such that

$$f_2(n_1, n_2, N, x_1, x_2) = f_1(n_1 + n_2, x_1) + n_2(x_2 - x_1)\varphi(n_1, n_2, N, x_1, x_2) \tag{1.3.1}$$

for any $(n_1, n_2, N, x_1, x_2) \in \mathcal{U}_2$. Then we have the following assertion which includes the claim of Theorem 2.2.10.

Theorem A.3.1. *The following conditions are equivalent:*
(1) *f_2 has an associated generating function.*
(2) *$\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_1)$ depends only on the values $n_1 + n_2$, N and x_1.*
(3) *Set*

$$H(n_1, n_2, N, x_1) = n_2\varphi(n_1, n_2, N, x_1, x_1) + n_1\varphi(n_2, n_1, N, x_1, x_1).$$

Then H depends only on the values $n_1 + n_2$, N and x_1.
(4) *Define*

$$\begin{aligned}G_*(n_1, n_2, N, x_1, x_2, y) &= f_1(n_1 + n_2, N, y)\\ &+ n_2(x_2 - y)\varphi(n_1, n_2, N, x_1, x_2) + n_1(x_1 - y)\varphi(n_2, n_1, N, x_2, x_1).\end{aligned} \tag{1.3.2}$$

Then G_* is a generating function associated with f_2.

The function G_* defined in (1.3.2) may be thought of as the canonical generating function associated with f_2. Note that there exists infinitely many generating functions associated with f_2 because

$$G_*(n_1, n_2, N, x_1, x_2, y) + c(x_2 - x_1)^2(y - x_1)(y - x_2)$$

is also a generating function associated with f_2 for any $c \in \mathbb{R}$ if G_* is so.

Proof of Theorem A.3.1. (1) ⇒ (2) Let G be a generating function associated with f_2. Then by (G3),

$$\begin{aligned}-\Theta(n_1, n_2, N, x_1, x_2) &= G(n_1, n_2, N, x_1, x_2, x_1) - G(n_2, n_1, N, x_2, x_1, x_2)\\ &= G(n_1, n_2, N, x_1, x_2, x_1) - G(n_1, n_2, N, x_1, x_2, x_2).\end{aligned}$$

Hence we have

$$-\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_1) = \frac{\partial G}{\partial y}(n_1, n_2, N, x_1, x_1, x_1).$$

On the other hand, by (G2), $G(n_1, n_2, N, x_1, x_1, y)$ only depends on the values n_1+n_2, N, x_1 and y and hence so does $\frac{\partial G}{\partial y}(n_1, n_2, N, x_1, x_1, y)$. Therefore, we have (2).
(2) ⇒ (3) By (1.3.1),

$$-\frac{\partial \Theta}{\partial x_2}(n_1, n_2, N, x_1, x_1) = -\frac{\partial f_1}{\partial x_1}(n_1 + n_2, x_1) + H(n_1, n_2, N, x_1, x_1).$$

Hence by (2), one sees that $H(n_1, n_2, N, x_1, x_2)$ only depends on the values $n_1 + n_2$, N and x_1.
(3) ⇒ (4) It is easy to see that G_* satisfies (G3). Since

$$G_*(n_1, 0, N, x_1, x_2, x_1) = f_1(n_1, N, y),$$

we have (G1). The fact that

$$G_*(n_1, n_2, N, x_1, x_1, y) = f_1(n_1 + n_2, N, y) + (x_1 - y)H(n_1, n_2, N, x_1)$$

immediately implies that (G2) holds if (3) is satisfied. Moreover,

$$\begin{aligned} G_*(n_1, n_2, N, x_1, x_2, x_1) &= f_1(n_1 + n_2, N, x_1) \\ &\quad + n_2(x_2 - x_1)\varphi(n_1, n_2, N, x_1, x_2) = f_2(n_1, n_2, N, x_1, x_2). \end{aligned}$$

Thus we have shown that G_* is a generating function associated with f_2.
(4) ⇒ (1) This is obvious. □

A.4 Proof of Theorem 2.2.14

In this subsection, we prove Theorem 2.2.14. The equation in question is (2.1.8). Note that Lemma A.1.2 is still true in this example. Let I be the 2×2 identity matrix. Using the same notations as A.1, we see that

$$\begin{aligned} &v_* = (1, 1), \\ &L(x_*) = \{(n_1, n_2, 1, x_*, x_*) \mid n_1 \geq 0, n_2 \geq 0, n_1 + n_2 = 1\}, \\ &J_1 = I, \\ &P = I, \end{aligned}$$

where J_1 and P have appeared in the proof of Lemma A.1.1. Consequently one see that

$$T_\epsilon = \left\{(n_1, n_2, N) \;\middle|\; \sqrt{(n_1 + n_2 - 1)^2 + (N - 1)^2} \leq \epsilon\right\} \cap \mathcal{U}_2.$$

Since the variable N dose not appear in the equations of n_1 and n_2, we only consider the first two equations on n_1 and n_2 in this section. Furthermore, for ease of notations, we write $x = n_1$, $y = n_2$ and $\alpha = x_2 - x_1$. As a result, our equation is

$$\begin{aligned} \frac{dx}{dt} &= x\big(1 - (x+y) + \alpha y(c - ax - by)\big) \\ \frac{dy}{dt} &= y\big(1 - (x+y) - \alpha x(c - ay - bx)\big). \end{aligned} \tag{1.4.1}$$

If $\widehat{T_\epsilon}$ and $\widehat{L}(x_*)$ are the projections of T_ϵ and $L(x_*)$ to (x, y)-plane respectively, then $\widehat{L}(x_*) = \{(x, y) | x \geq 0, y \geq 0, x + y = 1\}$ and

$$\widehat{T_\epsilon} = \{(x, y) \mid x \geq 0, y \geq 0, 1 - \epsilon \leq x + y \leq 1 + \epsilon\}.$$

By Lemma A.1.2, for sufficiently small ϵ, there exists $\delta > 0$ such that if $|\alpha| \leq \delta$, then $\widehat{T_\epsilon}$ is invariant with respect to the system of ODE's (1.4.1).

In case $(b - c)(a + b - 2c) > 0$, using (2.2.23), we can easily verify either (2.2.2) or (2.2.3) of Theorem 2.2.3. So, it is enough to consider the case where $(b - c)(a + b - 2c) < 0$. This case is subdivided into

$$(a + b - 2c) > 0 \text{ and } b - c < 0 \Leftrightarrow a > \frac{a+b}{2} > c > b \tag{Case 1}$$

and

$$(a + b - 2c) < 0 \text{ and } b - c > 0 \Leftrightarrow a < \frac{a+b}{2} < c < b \tag{Case 2}$$

Since both cases can be dealt with analogous methods, we are going to study one of them. Namely, we fix $a, b, c \in \mathbb{R}$ satisfying (Case 2) from now on.

Definition A.4.1. *Set* $U = \{(x, y) \mid x + y > 0\}$. *Define* $\tau : U \to \mathbb{R}^2$ *by*

$$\tau(x, y) = \Big(x + y, \frac{x - y}{x + y}\Big)$$

By using the polar coordinate $(x, y) = (r\cos t, r\sin t)$, where $(r, t) \in (0, \infty) \times (-\frac{\pi}{4}, \frac{3\pi}{4})$, it follows that

$$\tau(r\cos t, r\sin t) = \Big(r\cos\big(t - \frac{\pi}{4}\big), -\tan\big(t - \frac{\pi}{4}\big)\Big).$$

Set $U_\lambda = \{(r\cos t, r\sin t) \mid r > 0, t \in (\frac{\pi}{4} - \lambda, \frac{\pi}{4} + \lambda)\}$ for $\lambda \in (0, \frac{\pi}{2}]$. Then one can immediately verify the next lemma by direct calculation.

Lemma A.4.2. *For any* $\lambda \in (0, \frac{\pi}{2})$*,* τ *is a diffeomorphism between* U_λ *and* $(0, \infty) \times (-\tan\lambda, \tan\lambda)$*.*

Now if $(X, Y) = \tau(x, y)$, then the system of ODE's on (x, y), (1.4.1), is transformed into

$$\begin{aligned} \frac{dX}{dt} &= F_1(X, Y, \alpha) \\ \frac{dY}{dt} &= F_2(X, Y, \alpha), \end{aligned} \tag{1.4.2}$$

where

$$\begin{aligned} F_1(X, Y, \alpha) &= X(1 - X) + \frac{1}{4}\alpha(b - a)(1 - Y^2)X^3 Y \\ F_2(X, Y, \alpha) &= \frac{1}{4}\alpha X(1 - Y^2)\big(2c - (a + b)X + (a - b)XY^2\big). \end{aligned}$$

Define

$$\begin{aligned} G_1(X, Y, \alpha) &= 1 - X + \frac{1}{4}\alpha(b - a)(1 - Y^2)X^2 Y \\ G_2(X, Y) &= 2c - (a + b)X + (a - b)XY^2. \end{aligned}$$

Then $F_1(X, \alpha) = XG_1(X, \alpha)$ and $F_2(X, \alpha) = \frac{1}{4}\alpha X(1 - Y^2)G_2(X, Y)$.

From now on, we are going to study (1.4.2) on $\mathbb{R} \times (0, \infty)$. In particular, the original domain $[0, \infty) \times [0, \infty)$ of (1.4.1) corresponds to $[0, \infty) \times [-1, 1]$. Furthermore, since

$$\tau(\widehat{T_\epsilon}) = [1 - \epsilon, 1 + \epsilon] \times [-1, 1],$$

for sufficiently small ϵ, there exists δ such that if $|\alpha| \le \delta$, then $[1 - \epsilon, 1 + \epsilon] \times [-1, 1]$ is invariant with respect to the system of ODE's (1.4.2). Hereafter in this appendix, we choose ϵ and δ in this manner. In addition, we are going to adopt values of ϵ and δ to the coming circumstances several times in the course of our discussion.

Note that $(1, 1)$ (resp. $(1, -1)$) corresponds to the resident dominant (resp. the mutant dominant) equilibrium point. The Jacobian of the right-hand side of (1.4.2) at $(1, \pm 1)$ is

$$\begin{pmatrix} -1 & \frac{1}{2}\alpha(a - b) \\ 0 & \pm\alpha(b - c) \end{pmatrix}.$$

Hence if $\alpha > 0$ (reps. $\alpha < 0$), then $(1, 1)$ is locally unstable (resp. stable) and $(1, -1)$ is locally stable (resp. unstable).

Set $I_\epsilon = [1 - \epsilon, 1 + \epsilon] \times [-1, 1]$ and $I_\epsilon^o = (1 - \epsilon, 1 + \epsilon) \times (-1, 1)$. Next we are going to search equilibrium points of (1.4.2) inside I_ϵ.

Lemma A.4.3.

$$\Gamma(Y,\alpha) = \frac{2}{1+\sqrt{1-\alpha(b-a)(1-Y^2)Y}}$$

and

$$\Lambda_\pm(X) = \pm\sqrt{\frac{2c}{b-a}\frac{1}{X} - \frac{a+b}{b-a}}.$$

Then, for sufficiently small $\epsilon > 0$*, there exists* $\delta > 0$ *such that the following statements (1), (2) and (3) hold.*
(1) $\Lambda_\pm$ *are well-defined as functions on* $[1-\epsilon, 1+\epsilon]$ *and, for* $(X,Y) \in I^o_\epsilon$*,* $F_2(X,Y,\alpha) = 0$ *if and only if* $Y = \Lambda_\pm(X)$*.*
(2) Γ *is well-defined as a function on* $[-1,1] \times (-\delta,\delta)$ *and* $\Gamma([-1,1] \times (-\delta,\delta)) \subseteq [1-\epsilon, 1+\epsilon]$*. Moreover, for* $(X,Y) \in I^o_\epsilon$*,* $F_1(X,Y,\alpha) = 0$ *if and only if* $X = \Gamma(Y,\alpha)$*.*
(3) For any $\alpha \in (-\delta,\delta)$*, there exist a unique* $\Psi_+(\alpha) \in (0,1)$ *such that*

$$\Psi_+(\alpha) = \Lambda_+(\Gamma(\Psi_+(\alpha),\alpha))$$

and a unique $\Psi_-(\alpha) \in (-1,0)$ *such that*

$$\Psi_-(\alpha) = \Lambda_-(\Gamma(\Psi_-(\alpha),\alpha))$$

Moreover, define $\Phi_\pm(\alpha) = \Gamma(\Psi_\pm(\alpha))$ *and set* $p_\pm(\alpha) = (\Phi_\pm(\alpha), \Psi_\pm(\alpha))$*. Then*
(3a) *The function* $p_\pm : (-\delta,\delta) \to I^o_\epsilon$ *is* C^1*-class.*
(3b)

$$p_\pm(0) = \left(1, \pm\sqrt{\frac{a+b-2c}{a-b}}\right)$$

(3c) *If* $\alpha \neq 0$*, then* $p_+(\alpha)$ *and* $p_-(\alpha)$ *are all the equilibrium points of* (1.4.2) *in* I^o_ϵ*.*
(3d) *For any* $\alpha \in (-\delta,\delta)$*,*

$$(\Phi_-(-\alpha), \Psi_-(-\alpha)) = (\Phi_+(\alpha), -\Psi_+(\alpha)).$$

(3e) $\frac{d\Phi_\pm}{d\alpha}(\alpha) > 0$ *for any* $\alpha \in (-\delta,\delta)$*.*

Proof. (1) Note that $\Lambda_\pm$ does not depend on α. Since

$$-1 < \Lambda_-(1) < 0 < \Lambda_+(1) < 1,$$

choosing sufficiently small $\epsilon > 0$, we see that $\Lambda_-([1-\epsilon, 1+\epsilon]) \subseteq (-1, 0)$ and $\Lambda_+([1-\epsilon, 1+\epsilon]) \subseteq (0, 1)$. Furthermore, for $(X, Y) \in I_\epsilon^o$, $F_2(X, Y, \alpha) = 0$ if and only if $G_2(X, Y) = 0$. Since $G_2(X, Y) = 0$ if and only if $Y = \Lambda_\pm(X)$, the desired conclusion is verified.

(2) Since $\Gamma(Y, 0) = 1$ for any Y, it follows that $\Gamma([-1, 1] \times (-\delta, \delta)) \subseteq [1 - \epsilon, 1+\epsilon]$ for sufficiently small $\delta > 0$. For $(X, Y) \in I_\epsilon^o$, $F_1(X, Y, \alpha) = 0$ if and only if $G_1(X, Y, \alpha) = 0$. Since $G_1(X, Y, \alpha) = 0$ if and only if $X = \Gamma(Y, \alpha)$, we obtain the desired conclusion.

(3) Note that

$$\frac{\partial \Gamma}{\partial Y} = \frac{\alpha(b-a)(1-3Y^2)}{(1+\sqrt{1-\alpha(b-a)(1-Y^2)Y})^2\sqrt{1-\alpha(b-a)(1-Y^2)Y}} \tag{1.4.3}$$

and

$$\frac{d\Lambda_+}{dX} = -\frac{c}{(b-a)\Lambda_+(X)X^2}. \tag{1.4.4}$$

Since

$$\frac{\partial \Lambda_+ \circ \Gamma}{\partial Y}(Y, \alpha) = \frac{d\Lambda_+}{dX}(\Gamma(Y, \alpha))\frac{\partial \Gamma}{\partial Y}(Y, \alpha),$$

due to (1.4.3), we can choose $\delta > 0$ so that

$$\sup_{Y \in [-1,1], |\alpha| \leq \delta} \left| \frac{\partial \Lambda_+ \circ \Gamma}{\partial Y}(Y, \alpha) \right| \leq \frac{1}{2}. \tag{1.4.5}$$

Fix $\alpha \in (-\delta, \delta)$. Then as a function of Y, $\Lambda_+ \circ \Gamma$ is contractive on $[-1, 1]$. Hence the contraction mapping theorem shows that $\Lambda_+ \circ \Gamma$ has a unique fixed point in $[-1, 1]$. Let denote the unique fixed point by $\Psi_+(\alpha)$ and set $\Phi_+(\alpha) = \Gamma(\Psi_+(\alpha), \alpha)$. Then

$$\Lambda_+ \circ \Gamma(Y, \alpha) - Y = 0$$

for any $\alpha \in (-\delta, \delta)$. (1.4.5) yields

$$\frac{\partial(\Lambda_+ \circ \Gamma - Y)}{\partial Y}(\Psi_+(\alpha), \alpha) \neq 0.$$

Therefore, the implicit function theorem implies that Ψ_+ and Φ_+ are C^1-class functions. The statements (3b) and (3c) are straight forward. Again using the implicit function theorem, we verify (3d). For $\Psi_-(\alpha)$ and $\Phi_-(\alpha)$, entirely the same discussion yields the desired statements. Since $\Lambda_- = -\Lambda_+$ and

$$(\Gamma(Y, -\alpha) - 1) = -(\Gamma(Y, \alpha) - 1),$$

we have (3d). □

Due to the duality between the case where $\alpha > 0$ and the case where $\alpha < 0$, it is enough to study the case where $\alpha > 0$. In this case, if $K_\epsilon = [1-\epsilon, 1+\epsilon] \times [0,1]$ and $K_\epsilon^o = (1-\epsilon, 1+\epsilon) \times (0,1)$, then both K_ϵ and K_ϵ^o are invariant with respect to (1.4.2).

The following theorem suffices a proof of Theorem 2.2.14.

Theorem A.4.4. *Assume $\alpha > 0$. For any $(X_0, Y_0) \in K_\epsilon^o$, the solution of* (1.4.2) *starting from (X_0, Y_0) converges to $p_+(\alpha)$ as $t \to \infty$.*

To prove the above theorem, we use the following lemma.

Lemma A.4.5. *Assume $\alpha > 0$. Then there exists no periodic solution of* (1.4.2) *contained in K_ϵ^o.*

Proof. Suppose there exists a periodic orbit contained in K_ϵ^o which is not trivial, i.e. it is not a single point but homeomorphic to the circle. Let C be the periodic orbit and let D be the bounded domain whose boundary is C. Then the time-1 map ϕ_1 given by $\phi_1(X(t), Y(t)) = (X(t+1), Y(t+1))$ is a continuous map from D to itself. Hence by the Brouwer fixed point theorem, it has a fixed point inside D. Since $p_+(\alpha)$ is the only equilibrium point in K_ϵ^o, we conclude that $p_+(\alpha)$ belongs to the interior of D.

Next we divide K_ϵ^1 into four regions K_1, K_2, K_3 and K_4 defined as

$$\begin{aligned}
K_1 &= \{(X,Y) \mid Y \geq \Lambda_+(X), X \geq \Gamma(Y,\alpha)\} \cap K_\epsilon \\
K_2 &= \{(X,Y) \mid Y \geq \Lambda_+(X), X \leq \Gamma(Y,\alpha)\} \cap K_\epsilon \\
K_3 &= \{(X,Y) \mid Y \leq \Lambda_+(X), X \leq \Gamma(Y,\alpha)\} \cap K_\epsilon \\
K_4 &= \{(X,Y) \mid Y \leq \Lambda_+(X), X \geq \Gamma(Y,\alpha)\} \cap K_\epsilon
\end{aligned}$$

and define four curves C_{12}, C_{23}, C_{34} and C_{41} as

$$\begin{aligned}
C_{12} &= \{(\Gamma(Y,\alpha), Y) \mid Y \in [\Psi_+(\alpha), 1]\} \\
C_{23} &= \{(X, \Lambda_+(X)) \mid X \in [1-\epsilon, \Phi_+(\alpha)]\} \\
C_{34} &= \{(\Gamma(Y,\alpha), Y) \mid Y \in [0, \Psi_+(\alpha)]\} \\
C_{41} &= \{(X, \Lambda_+(X)) \mid X \in [\Phi_+(\alpha), 1+\epsilon]\}.
\end{aligned}$$

Then it follows that $C_{ij} = K_i \cap K_j$ for any $(i,j) \in \{(1,2),(2,3),(3,4),(4,1)\}$. Moreover, one can see the exact direction of the vector field $\begin{pmatrix} F_1(X,Y) \\ F_2(X,Y) \end{pmatrix}$ on each C_{ij}. Namely, it follows that

$$\begin{pmatrix} F_1 \\ F_2 \end{pmatrix} = \begin{pmatrix} 0 \\ - \end{pmatrix} \text{ on } C_{12}, \quad \begin{pmatrix} + \\ 0 \end{pmatrix} \text{ on } C_{23}, \quad \begin{pmatrix} 0 \\ + \end{pmatrix} \text{ on } C_{34}, \quad \begin{pmatrix} - \\ 0 \end{pmatrix} \text{ on } C_{41}.$$

Furthermore, since $p_+(\alpha)$ belongs to the interior of D, it follows that

$$C \cap \big(K_i \backslash \{p_+(\alpha)\}\big) \neq \emptyset \tag{1.4.6}$$

for any $i = 1, 2, 3, 4$ and

$$C \cap \big(C_{ij} \backslash \{p_+(\alpha)\}\big) \neq \emptyset \tag{1.4.7}$$

for any $(i, j) \in \{(1, 2), (2, 3), (3, 4), (4, 1)\}$.

Now we have four cases according to the signs of c and $\Psi_+(0) - \frac{1}{\sqrt{3}}$. Note that by (1.4.3), $\Gamma(Y)$ is monotonically increasing in $[0, \frac{1}{\sqrt{3}}]$ and monotonically decreasing in $[\frac{1}{\sqrt{3}}, 1]$.

Case I $c \geq 0$ and $\Psi_+(0) > \frac{1}{\sqrt{3}}$: By (1.4.4), Λ_+ is monotonically decreasing on $[1 - \epsilon, 1 + \epsilon]$. Since $\Psi_+(0) > \frac{1}{\sqrt{3}}$, it follows that $\Psi + (\alpha) > \frac{1}{\sqrt{3}}$ as well for sufficiently small α. Hence considering the dynamics on the boundaries C_{12} and C_{23}, we see that the domain K_2 is invariant. By (1.4.6) for $i = 2$, the periodic orbit C must be included in K_2. This contradicts to (1.4.6) for $i = 4$. Thus, there exists no periodic orbit contained in K_ϵ^o (See Figure 1.4.1).

Case II $c \geq 0$ and $\Psi_+(0) \leq \frac{1}{\sqrt{3}}$: As in Case I, Λ_+ is monotonically decreasing on $[1 - \epsilon, 1 + \epsilon]$. Since $\Psi_+(0) \leq \frac{1}{\sqrt{3}}$, we see that $\Psi_+(\alpha) < \frac{1}{\sqrt{3}}$ for sufficiently small $\alpha > 0$. Set

$$C_{12}^1 = \left\{ (\Gamma(Y), Y) \;\middle|\; Y \in [\Psi_+(\alpha), \frac{1}{\sqrt{3}}] \right\}.$$

Then if a solution of (1.4.2) exits K_2, then it exits K_2 from C_{12}^1 and enters K_1. In particular, so does the periodic orbit C (See Figure 1.4.2). Now we start chasing the periodic orbit. Let

$$Y_1 = \max \left\{ Y \;\middle|\; (X, Y) \in C_{12}^1 \cap C \right\}.$$

Considering the dynamics on K_1, we obtain

$$C \cap K_1 \subseteq \{(X, Y) \mid X \in [\Phi_+(\alpha), \Gamma(Y_1, \alpha)]\} \cap K_1.$$

Set $X_1 = \Gamma(Y_1, \alpha)$ and define

$$C_{41}^1 = \{(X, \Lambda_+(X)) \mid X \in [\Phi_+(\alpha), X_1]\}.$$

Then the periodic orbit exits K_1 from C_{41}^1, enters K_4 and stays in

$$K_4 \cap \{(X, Y) \mid Y \in [\Lambda_+(X_1), \Psi_+(\alpha)]\}.$$

Let us continue chasing the periodic orbit C. Set $Y_2 = \Lambda_+(X_1)$ and define

$$C^1_{34} = \{(\Gamma(Y,\alpha), Y) \mid Y \in [Y_2, \Psi_+(\alpha)]\}\,.$$

Then the periodic orbit C exits K_4 from C^1_{34}, enters K_3 and stays in

$$K_3 \cap \{(X,Y) \mid X \in [\Gamma(Y_2,\alpha), \Phi_+(\alpha)]\}\,.$$

Set $X_2 = \Gamma(Y_2,\alpha)$ and define

$$C^1_{23} = \{(X, \Lambda_+(X)) \mid X \in [X_2, \Phi_+(\alpha)]\}\,.$$

Then the periodic orbit C exits K_3 from C^1_{23}, enters K_2 and stays in

$$K_2 \cap \{(X,Y) \mid Y \in [\Psi_+(\alpha), \Lambda_+(X_2)]\}\,.$$

Finally, by the definition of Y_1, it follows that

$$Y_1 \leq \Lambda_+(X_2) = \Lambda_+(\Gamma(\Lambda_+(\Gamma(Y_1)))) = (\Lambda_+ \circ \Gamma)^2(Y_1)$$

Due to (1.4.5), however, we have

$$\frac{1}{4}(Y_1 - \Psi_+(\alpha)) \geq (\Lambda_+ \circ \Gamma)^2(Y_1) - \Psi_+(\alpha).$$

Thus there exists no periodic orbit contained in K^o_ϵ.

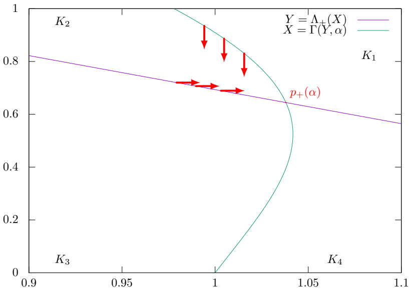

Figure 1.4.1: Case I

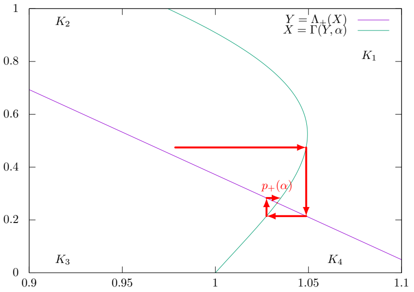

Figure 1.4.2: Case II

Case III $c < 0$ and $\Psi_+(0) \geq \frac{1}{\sqrt{3}}$: In this case, since $c < 0$, (1.4.5) implies that Λ_+ is monotonically increasing on $[1-\epsilon, 1+\epsilon]$. Since $\Psi_+(0) \geq \frac{1}{\sqrt{3}}$, we have $\Psi_+(\alpha) > \frac{1}{\sqrt{3}}$. Define $C^2_{34} = \left\{(\Lambda(Y,\alpha), Y) \,\middle|\, Y \in [\frac{1}{\sqrt{3}}, \Psi_+(\alpha)]\right\}$. Then if a solution of (1.4.2) exits K_3, then it exits K_3 from C^2_{34}. The rest of the arguments are entirely similar to Case II.

Case IV $c < 0$ and $\Psi_+(0) < \frac{1}{\sqrt{3}}$: As in Case III, Λ_+ is monotonically increasing on $[1-\epsilon, 1+\epsilon]$. Since $\Psi_+(0) < \frac{1}{\sqrt{3}}$, we have $\Psi_+(\alpha) < \frac{1}{\sqrt{3}}$ for sufficiently small $\alpha > 0$. In this case, K_3 is invariant and the rest of the arguments are entirely the same as Case I. $\square$

Proof of Theorem A.4.4. Let $(X_0, Y_0) \in K_\epsilon^o$ and let $(X(t), Y(t))$ be the solution of (1.4.2) satisfying $(X(0), Y(0)) = (X_0, Y_0)$. By the Poincaré-Bendixson theorem, the ω-limit set of $\{(X(t), Y(t))\}_{t>0}$ is a periodic orbit or an equilibrium point. By Lemma A.4.5, it follows that the ω-limit set is not a periodic orbit. Hence it is an equilibrium point. Now there are only two equilibrium points in K_ϵ^o which are $(1,1)$ and $(\Phi_+(\alpha), \Psi_+(\alpha))$. Since $(1,1)$ is locally unstable and its stable manifold is $Y = 1$, the equilibrium point $(1,1)$ can not be the ω-limit set. Therefore the ω-limit set must be $(\Phi_+(\alpha), \Psi_+(\alpha))$. $\square$

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