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ADAPTIVE DYNAMICS OF RESOURCE SPECIALIZATION

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Abstract

Ecological specialization in resource utilization has various facades ranging from nutritional resources via host use of parasites or phytophagous insects to local adaptation in different habitats. Therefore, the evolution of specialization affects the evolution of most other traits, which makes it one of the core issues in the theory of evolution. Hence, the evolution of specialization has gained enormous amounts of research interest, starting already from Darwin's Origin of species in 1859. Vast majority of the theoretical studies has, however, focused on the mathematically most simple case with well-mixed populations and equilibrium dynamics. This thesis explores the possibilities to extend the evolutionary analysis of resource usage to spatially heterogeneous metapopulation models and to models with non-equilibrium dynamics. These extensions are enabled by the recent advances in the field of adaptive dynamics, which allows for a mechanistic derivation of the invasion-fitness function based on the ecological dynamics. In the evolutionary analyses, special focus is set to the case with two substitutable renewable resources. In this case, the most striking questions are, whether a generalist species is able to coexist with the two specialist species, and can such trimorphic coexistence be attained through natural selection starting from a monomorphic population. This is shown possible both due to spatial heterogeneity and due to non-equilibrium dynamics. In addition, it is shown that chaotic dynamics may sometimes inflict evolutionary suicide or cyclic evolutionary dynamics. Moreover, the relations between various ecological parameters and evolutionary dynamics are investigated. Especially, the relation between specialization and dispersal propensity turns out to be counter-intuitively non-monotonous. This observation served as inspiration to the analysis of joint evolution of dispersal and specialization, which may provide the most natural explanation to the observed coexistence of specialist and generalist species.

Tiivistelmä

Tässä työssä tutkitaan ekologisten resurssien käytön erikoistumista. Matemaattisen mallinnuksen näkökulmasta resursseiksi voidaan ravinnon ja suojapaikkojen lisäksi mieltää myös esimerkiksi loiseläinten isännät tai sirpaloituneen ympäristön erilaiset asuinalueet eli laikut. Tätä monimuotoista alaa on tutkittu runsaasti, mutta keskittyen lähes yksinomaan matemaattisesti yksinkertaisimpiin malleihin, joissa eliöt käyttävät vain yhtä homogeenista elinaluetta ja populaatiodynamiikan attraktori on kiintopiste. Tässä työssä tutkitaan jaksollisen tai kaoottisen populaatiodynamiikan sekä metapopulaatiorakenteen vaikutuksia erikoistumisen evoluutioon. Evoluution mallintaminen tapahtuu tässä työssä adaptiivisen dynamiikan keinoin eli johtaen kelpoisuusfunktio mekanistisesti ekologisesta dynamiikasta. Työssä keskitytään ennen kaikkea tapaukseen, jossa organismi voi käyttää kahta vaihtoehtoista resurssia, ja tutkitaan, milloin monomorfisesta populaatiosta alkava evoluutio voi johtaa trimorfiseen yhteiseloon, jossa generalisti kykenee elämään yhdessä kahden spesialistin kanssa, vaikka kumpikin spesialisti hyödyntää yksittäistä resurssia generalistia tehokkaammin. Trimorfinen yhteiselo ei ole mahdollista yksittäisessä homogeenisessa elinympäristössä, jos populaatiodynamiikan attraktori on kiintopiste. Tässä työssä osoitetaan, että monomorfisesta populaatiosta alkava evoluutio voi johtaa trimorfiseen yhteiseloon silloin, jos homogeenisen elinympäristön populaatiodynamiikka on jaksollista tai kaoottista, sek silloin, jos homogeenisen elinalueen sijaan tarkastellaankin metapopulaatiota. Lisäksi osoitetaan, että kaoottinen populaatiodynamiikka voi joskus johtaa sykliseen evolutiiviseen dynamiikkaan tai jopa koko populaation tuhoon evolutiivisen itsemurhan kautta. Työssä tutkitaan myös ekologisen mallin eri parametrien vaikutusta erikoistumisen evoluutioon. Muuttoliikkeen vaikutus erikoistumisen evoluutioon havaitaan intuition vastaisesti epämonotoniseksi, minkä innoittamana syvennytään myös muuttotodennäköisyyden ja erikoistumisen yhteisevoluutioon, joka todetaan kenties luontaisimmaksi selitykseksi spesialistien ja generalistien trimorfiselle yhteiselolle.

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List of original publications

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   population dynamics
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Part I
General theory

Contents

1 Introduction

Ecological specialization is one of the core issues in the study of evolution. Specialization, often viewed in the form of local adaptation, affects the evolutionary dynamics of any life-history trait. Therefore, specialization has been a topic for a wide range of research. Already Darwin (1859) used the existence of various forms of specialization and local adaptation as evidence when arguing that species evolve in nature. Since then, the amount of research work focused on the different aspects of the evolution of specialization has increased enormously.

When evolutionary biology is popularized, the term ”specialized” often refers to species with extraordinary or bizarre features, e.g., tremendous horns or other extravagant armament. As noted by Amadon (1943), these extraordinary traits may sometimes be evolutionarily extremely important by allowing the species, or clades, to obtain abilities to utilize completely new niche types. Most obvious example of this process was presented by Huxley (1868, 1870) who viewed birds as glorified dinosaurian reptiles with the extraordinary ability to fly.

However, usually in the evolutionary biology literature, the term ”specialization” is used in the situations where a species is, in principle, capable of using two or more alternative resources, but there is a trade-off between the abilities to use these resources (Futuyma and Moreno, 1988; Jaenike, 1990; Scheiner, 1993; Abrams, 2000b; Ravigné et al., 2009; Poisot et al., 2011; Forister et al., 2012). Generalists use all, or several, of these resources whereas specialists exclude some of the resources in order to be more efficient in using the others. The term ”resources” may here be interpreted rather generally. It may refer to, for example, nutritional resources such as different plants eaten by a herbivore, different prey species captured by a predator, different hosts of a parasite, different possible habitats in a spatially heterogeneous landscape, etc. For field-biologically inclined discussions concerning the concepts of specialism, generalism and the nature and existence trade-offs, see, e.g., Fry (1996, 2003), Kneitel and Chase (2004), Loxdale et al. (2011) and Dennis et al. (2011).

Specialization, in this wide sense, is a part of the evolutionary dynamics of any other life history trait. Most of all, the evolution of specialization, in the form of local adaptation, interacts with the evolution of dispersal: the better an individual is adapted to its prevailing local conditions, the higher is the risk that this individual, if dispersing, ends in a habitat with less favorable conditions (Clobert et al., 2001). The relation between specialization and dispersal, however, is more complicated than this simplification, especially in the presence of local disasters or other temporal variations that may harm, or even wipe out, local populations (Nurmi and Parvinen, 2008, 2011).

From the point of view of conservation biology, it is important to understand this relation, since, on one hand, increasing habitat fragmentation makes the species and their local populations more vulnerable to temporal disorders (Schoener and Spiller, 1987; Root, 1998; Casagrandi and Gatto, 1999), and on the other hand, habitat loss and fragmentation have an outstanding effect on the loss of biodiversity worldwide (Barbault and Sastrapradja, 1995; Debinski and Holt, 2000; Sih et al., 2000; Fahrig, 2003), and the degree of specialization affects crucially both the consequences of habitat fragmentation and the global extinction risk of species (Turner, 1996; McKinney, 1997; Henle et al., 2004; Colles et al., 2009; Brückmann et al., 2010). Altogether, it is of great importance to understand the complex interplay between the evolutionary dynamics of specialization and dispersal in the presence of temporal variations in order be able to study their evolutionary dynamics in heterogeneous and fragmented environments. This thesis aims to explore this interplay, and thus, to provide tools for understanding the possible evolutionary responses for habitat degradation and fragmentation.

However, this thesis has also another, equally important, objective: understanding the origins of biodiversity. This objective is targeted, in the case of two alternative resources, via one specific theoretical question: under which conditions can an initially monomorphic species (i.e., a species that comprises one type of individuals only) evolve to the trimorphic coexistence of a generalist type with two specialists types. This question has recently been vividly discussed (Wilson and Yoshimura, 1994; Egas et al., 2004; Abrams, 2006a,b). In this thesis, two mechanisms are being demonstrated and analyzed that allow an initially monomorphic population to evolve to the trimorphic coexistence of generalists and specialists. One of the mechanisms is based on the joint evolution of dispersal propensity and resource specialization (Nurmi and Parvinen, 2011), whereas the other builds on non-equilibrium population dynamics (Nurmi and Parvinen, 2013).

The main focus of this thesis is in the understanding of the evolution of resource usage in the case of two alternative resources and spatially heterogeneous environments. When the population is not well-mixed, the evolutionary analysis of any trait becomes rather cumbersome. Here, population dynamics in heterogeneous space are modeled by structured metapopulation models. The evolutionary analysis utilizes the adaptive dynamics approach. Below, these main tools, metapopulation models and adaptive dynamics are introduced.

In order to build metapopulation models suitable for evolutionary analysis, one first has to derive a model for the dynamics of the local populations based on individual-level processes, and then lift this model to the metapopulation level by book-keeping. After the general introductions of the metapopulation models and adaptive dynamics, this modeling process is introduced together with a metapopulation-level proxy for the invasion fitness.

Finally, the results of the evolutionary analyses are reviewed in the light of current conceptions of evolutionary dynamics of specialization. These results concentrate on the evolution of resource utilization in metapopulations, on the joint evolution of specialization and dispersal, and on evolution under non-equilibrium ecological dynamics.

2 Metapopulation models

2.1 Spatially heterogeneous models of ecological dynamics

In traditional models of ecology, it is assumed that all the individuals under consideration interact equally with each other, independent of their exact location. Based on this assumption, it is possible to assume that contact rates between individuals follow the law of mass action. For example in the case of predator–prey relationships, the rate at which prey is captured by the predators is often assumed to be linearly proportional to the rate of encounters between the prey individuals and the predator individuals. This rate, in turn, is proportional both to the prey density and to the density of prey-searching predators. Thus, all the prey individuals encounter identical predation pressure independent of the area they inhabit. This kind of population is often called well-mixed. Note that in the predator–prey example, the number of prey-searching predators is generally not directly proportional to the number of predators since the predators need time to capture, handle and digest the prey (nonlinear functional response).

However, natural populations are usually not well-mixed, and the environment, in which they live, is neither homogeneous nor of uniform quality. Sometimes, for example in the case of marine organisms, changes in the environmental quality occur continuously. In this case, the spatial heterogeneity encountered by the organisms can be described by a partial differential equation, and the modeler ends up using, e.g., reaction-diffusion models (Skellam, 1951; Levin, 1976; Gurtin and MacCamy, 1977; Holmes et al., 1994; Okubo and Levin, 2001). However, when terrestrial organisms are considered, changes in the environment rarely occur continuously. Instead, the suitable grazing and breeding areas of any species are usually distributed to patches surrounded by unsuitable areas. These suitable patches are called local habitats. Individuals within a local habitat interact almost exclusively with each other, and thus, form a local population. Only rough estimates of local population dynamics can be presented on the basis of models that deal solely with well-mixed populations. This is because the local populations interact by dispersal, which usually affects the local population dynamics in the patch. Once this dispersal is taken into account, one ends up with metapopulation dynamics (Hanski, 1998, 1999).

The term ”metapopulation” was first used by Levins (1969, 1970). In his terminology, a metapopulation is a collection of partially isolated local populations living in discrete habitat patches connected by dispersal. Levins assumed that the local habitat patches are prone to local disasters that may occasionally wipe out the local population. This results in empty habitat patches that may again become recolonized by immigrants arriving from the other patches. In the Levins’ metapopulation model, the local population dynamics within patches are completely omitted. Therefore, a patch may only have two alternative states: either the patch is occupied or it is empty and colonizable by immigrants. Moreover, the spatial configuration of the habitats, as well as differences between them, are neglected in the dispersal process. Furthermore, because of mathematical tractability, it is assumed that there are infinitely many local habitats.

2.2 The Levins’ model and other patch occupancy models

If one denotes the fraction of occupied patches by p and assumes that dispersers colonize empty patches with the rate c (”colonization rate”), and that occupied patches become empty with the rate d (”catastrophe rate”), then one can write the Levins’ metapopulation model as

$$\frac{dp}{dt} = cp(1-p) - dp,$$

where $1 - p$ is the fraction of empty patches (available for colonization). It is thus assumed that the amount of dispersers colonizing empty patches is directly proportional to the fraction p of occupied patches. The Levins’ model is obviously an oversimplification, and its main significance is that it provides an easily accessible viewpoint to the most important metapopulation-scale phenomenon: a species may persist even though all its subpopulations in local habitats are occasionally, but not simultaneously, destroyed by randomly occurring disasters (Hanski and Gilpin, 1997).

The Levins’ model, however, often maintains its mathematical tractability even with more realistic functional forms of colonization and catastrophe rates (Gotelli, 1991; Gotelli and Kelley, 1993; Hanski and Gyllenberg, 1993) or several different patch types (Horn and Mac Arthur, 1971; Levin, 1974, 1976). The assumption of infinitely many uniformly connected patches is more essential for the mathematical tractability. If it is dropped, the models usually can be analyzed only via simulations. Nevertheless, it is relatively easy, for a field biologist, to observe habitat patch connectivities, and to distinguish occupied and empty habitats. Thus, models based on the patch occupancies and non-uniform dispersal, such as the incidence function model by Hanski (1992, 1994a,b), provide widely used tools for field biology.

In the evolutionary analysis, however, the main drawback of the patch occupancy models is that they are usually built completely phenomenologically directly to the metapopulation level without considering the individual level processes at all. Therefore, these models enable only evolutionary analysis that is completely based on group selection (see, e.g., Van Valen (1971)). Natural selection, however, takes place at the level of individuals such that the membership of a group may only affect, but not completely determine, the fitness of an individual (Williams, 1966; Rueffler et al., 2006). Therefore, the analysis of evolutionary dynamics in heterogeneous landscapes is reasonable only in structured metapopulation models that are mechanistically underpinned on individual-level ecological dynamics (Geritz and Kisdi, 2012). Moreover, structured metapopulation models offer a unified and clarified approach to the situations in which multi-level selection takes place and the phenomenological definition of fitness functions is less straightforward (Wilson and Sober, 1994). In addition, the structured models allow also biologically more realistic theoretical analysis of the ecological dynamics.

2.3 Structured metapopulation models

Structured models involve at least some level of spatial heterogeneity, but still model explicitly the local population dynamics, which, in turn, are affected by dispersal. In a metapopulation model, each local population is assumed to be well-mixed. Simplest structured models comprise only two habitat patches. Let x_i and $f_i(x_i)$ denote, respectively, the local population density and the density-dependent per capita population growth rate in patch i, and furthermore, assume that individuals migrate from patch i

to patch j with rate e_{ij} and survive migration with probability π. Then, one can write down a continuous-time two-patch metapopulation model as (Freedman and Waltman, 1977; Hastings, 1983; Holt, 1985)

$$\begin{aligned}\frac{dx_1}{dt} =& f_1(x_1)x_1 - e_{12}x_1 + \pi e_{21}x_2 \\ \frac{dx_2}{dt} =& f_2(x_2)x_2 - e_{21}x_2 + \pi e_{12}x_1.\end{aligned} \tag{1}$$

Note that the generalization of these models to include any finite number of different patches is mathematically rather straightforward, but the analysis of the model and the field-biological determination of the ecological parameters become cumbersome.

Alternatively, a two-patch model may have discrete-time dynamics described by difference equations (Hastings, 1993; Gyllenberg et al., 1993). Despite its simplicity, a two-patch model may exhibit extremely complex ecological dynamics, which enables one to study the effects of dispersal on the stability of the population dynamics (Hastings, 1993; Gyllenberg et al., 1993; Ruxton et al., 1997; Kisdi, 2010). Moreover, the two-patch models offer the simplest possible framework for the analysis of source–sink population dynamics (Pulliam, 1988; Dias, 1996; Gyllenberg et al., 1996). The term ”source” refers to a habitat in which the local birth rate (or fecundity in discrete-time models) on average exceeds the death rate (probability), whereas in a sink population the death rate exceeds the birth rate. Thus, a sink population may persist only by the means of immigration from other patches. In metapopulations, abundant migration from high-quality patches may raise the local population density in low-quality patches such that, due to the density-dependent effects, the local death rate exceeds the local birth rate even though the local population would be viable also alone, with lower local population density however. This kind of patches were named ”pseudo-sinks” by Watkinson and Sutherland (1995).

Thus, a structure comprising sources and sinks or pseudo-sinks is natural to metapopulations. When considering the evolution of resource specialization, the source–sink structure is not the same for all individuals. Patches that are of high quality to a species that is specialized to one resource may be low-quality patches to a species specialized to another resource. In addition, the differences between patches usually appear smaller when they are observed by a generalist compared to the differences observed by a specialist. Moreover, if periodic or chaotic population-dynamical attractors are possible, different local populations of the same species may have qualitatively different population-dynamical attractors. Simultaneously, it is also possible that, even within a single patch, species with different specialization strategies encounter qualitatively different population-dynamical attractors.

Moreover, dispersal is a key ingredient in spatial population models with non-equilibrium attractors: intermediate dispersal propensity may stabilize the local population dynamics in the patches that would, in the absence of dispersal, exhibit periodic or chaotic population dynamics, but more abundant dispersal may have a synchronizing effect instead of a stabilizing one. Then again, the type of the population-dynamical attractor affects the evolution of dispersal propensity: if all the local population densities are at their equilibrium values, dispersal is selected against, but when the local population densities fluctuate, dispersal may become beneficial (Hastings, 1983; Parvinen, 1999), and furthermore, the dispersal propensity may even undergo evolutionary branching where the population splits into two morphs; one dispersing abundantly and the other scarcely (Doebeli and Ruxton, 1997; Parvinen, 1999).

As the evolution of specialization interacts significantly with that of dispersal, it is necessary to understand both the effects of dispersal on local population dynamics and the consequences of source–sink structures to be able to study the evolution of specialization in spatially heterogeneous environments (Ronce and Kirkpatrick, 2001; Nurmi and Parvinen, 2008, 2011, 2013).

When the number of local habitat patches is increased from two in the metapopulation model (1), the modeler has to consider the details of the dispersal process, since the dispersal rates (probabilities) and dispersal survival may be different for each pair of patches. The means of matrix calculus may enable the mathematical analysis of such models for some extent (Parvinen, 1999), but usually some mean-field approximation is necessary when modeling dispersal. For example, the patches may be assumed to be equally connected by dispersal (Levin et al., 1984; Cohen and Levin, 1991). Some general conclusions can also be drawn, if it is assumed that the habitat patches form a grid, and dispersal in this grid is distance-limited, for example, only to nearest neighbors. In this case, one ends up with coupled map lattices analyzed, e.g., by Kaneko (1992, 1998) and Karonen (2011). However, if one wishes to build a spatially explicit model, where all the connections between patches are taken into account, the only way to analyze the resulting model is via simulations that require careful parameter estimation (see, e.g., Hanski and Thomas (1994), Hanski et al. (1994) and Hanski and Ovaskainen (2003)).

The two-patch and n-patch models introduced above lack one essential feature included in the Levins' metapopulation model: the frequent but random catastrophes that occasionally wipe out local populations but leave the patches habitable and recolonizable. If the number of patches is finite, such catastrophes are liable to drive any population to extinction, at least in the evolutionary time-scale. There are, however, models with finite number of patches, where local conditions in patches alternate randomly, but these temporal variations are mild in the sense that local populations are not wiped out completely, which enables the viability of the population in the evolutionary time-scale (McPeek and Holt, 1992; Kisdi, 2002).

Altogether, in any model intended for evolutionary analysis, the assumption of randomly occurring disasters destroying entire local populations must be accompanied with the assumption of infinitely many patches. If one, in addition, assumes global dispersal ignoring the spatial arrangement of the patches, the model even becomes mathematically tractable (Hastings and Wolin, 1989; Hastings, 1991; Gyllenberg and Hanski, 1992, 1997; Gyllenberg et al., 1997). One can then assume that all the emigrating dispersers enter a disperser pool, from which they are distributed evenly to all of the patches. Let now D_n be the size per patch of the disperser pool at time n. If one now focuses on a single patch with population density x_n at time n, one can determine the local discrete-time dynamics as

$$x_{n+1} = C(n+1)(1-e)f(x)x_n + \pi D_n(s),$$

where the function f determines the local growth and survival within the patch. This function may vary from patch to patch. The parameters π and e determine, respectively, dispersal survival and the emigration probability of an individual during one time step. Furthermore, $C(n+1)$ is a random variable drawn from the Bernoulli distribution with parameter c.

It determines the occurrence of the local catastrophes, i.e.,

$$C(n+1) = \begin{cases} 1, & \text{if there is no local catastrophe in the focal} \\ & \text{patch after period } n \text{ (probability } 1-c\text{),} \\ 0, & \text{if a local catastrophe occurs} \\ & \text{after period } n \text{ (probability } c\text{).} \end{cases} \tag{2}$$

When there is only a finite number of different patch types, the dynamics of the disperser pool size can be heuristically defined as

$$D_n = \sum_m p_m \begin{pmatrix} \text{Expected number of emigrants} \\ \text{from a type } m \text{ patch at time } n \end{pmatrix},$$

where p_m is the fraction of type m patches. The actual calculation of D_n from this equation is rather demanding. However, in metapopulations with globally attracting fixed point equilibrium, one can neglect this calculation and solve D_n from a fixed point equation, since in the fixed point D_n has a constant value D and this value must be such that once a disperser enters a local population, the local clan it initiates, i.e., itself and all of its descendants, their descendants, etc, will on average produce exactly one new successful disperser before the clan is destroyed by the next catastrophe in the patch..

Below in section 4, this metapopulation model is adjusted for resource–consumer dynamics and the evolution of resource specialization of the consumers. Derivation of the local dynamics follows the guidelines given by Geritz and Kisdi (2004), and the calculation of invasion fitness (or more precisely a proxy for the metapopulation-level invasion-fitness) is based on the method by Parvinen (2006), who adapted the metapopulation reproduction ratio concept introduced by Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001) to discrete-time metapopulation models. However, before considering fitness in metapopulations, the adaptive dynamics framework is introduced as a general toolbox for modeling frequency- and density-dependent long-term evolution of continuous traits in ecologically realistic settings.

3 Adaptive dynamics

3.1 Historical background

In the days of Darwin (1859), the Mendelian genetics was not widely known, and thus, it was natural that all the evolutionary considerations took place at the phenotypic level: the traits that are beneficial for the reproduction and survival of an individual were simply predicted to become more common in nature. When the results of Mendel were rediscovered at the beginning of the 20th century (see, e.g., Fischer (1936)), the permanence of genetic material and the consequent discreteness of hereditary alteration first seemed to conflict with Darwin's ideas of gradual evolution (see, e.g., Mayr (1982)). This controversy was solved by the rise of population genetics conducted by Fischer (1930), Wright (1931) and Haldane (1932) and the resulting modern synthetic evolutionary theory (Dobzhansky, 1937; Huxley, 1942).

Mathematical population genetics considers evolution as fluctuations in the frequencies of different alleles or genotypes in populations. Besides the randomly occurring mutations and natural selection, these fluctuations are affected also by random genetic drift (especially in small populations) and gene flow caused by dispersal. Furthermore, the genetic architecture of the species affects the fluctuations via, e.g., epistasis, linkage, and recombination. Population-genetic models aim to model this genetic complexity in detail. A trade-off that is required to keep the models analyzable, is that the species' ecological framework must be assumed to be relatively simple. Therefore, despite the increasing knowledge on genetics, phenotypic models of evolution are still useful when pursuing ecological realism in evolutionary models and predictions.

Classical population genetics usually assume that a unique measure of fitness is directly attached to each possible trait combination, and furthermore, that this measure is independent of the traits of the rest of the population (Wright, 1932; Lande, 1976). This means that selection is assumed to be frequency- and density-independent and the fitness values of the possible trait combinations form a so-called fitness landscape, where evolution proceeds always uphill: a trait combination with given fitness can always outcompete the combinations with lower fitness, as well as it will be outcompeted once a trait combination with higher fitness appears.

This results in optimization models where evolution leads to a trait combination whose fitness value is a local maximum of the fitness landscape. With two-dimensional traits this process corresponds to finding the hill peaks on a topographical map that describes the fitness landscape. Note that if the mutations are assumed to be small in effect, evolution does not necessarily lead to the highest peak, but instead only the nearest local maximum is achieved.

The incorrectness of the assumption of frequency-independence was realized already in the early history of population genetics as it was noted that an allele or trait may benefit from being rare (Haldane, 1932; Lewontin, 1958; Ayala and Cambell, 1974). Most obviously, this assumption fails in the case where the fitness of an individual depends on pairwise interactions between conspecifics, such that the strategy (evolving trait) of the opponent affects the success of an individual. Then, the fitness value of any trait combination is not constant but depends on the trait frequencies in the population. This means, that the fitness landscape is not constant, but it depends on the frequencies of the different strategies in the resident population. This idea is included into the framework of evolutionary game theory introduced by Maynard Smith (1974, 1976, 1982).

In evolutionary game theory (Nowak and Sigmund, 2004), it is assumed that the fitness of an individual is affected by the individual's success in consecutive pairwise interactions with conspecifics. In each encounter, an individual may select from several behavioral patterns, e.g., escalate a conflict, display, negotiate or withdraw. These patterns are the traits, the evolution of which evolutionary game theory considers. An individual may always use the same behavioral pattern. This is called a pure strategy. However, an individual may also use a mixed strategy, i.e., use different behavioral patterns with different probabilities. In this case, the strategy vector of an individual determines these probabilities. In a specific encounter, the payoffs that the interacting individuals obtain (or losses they suffer) are determined by the behavioral patterns (pure strategies) used by the interacting individuals in this encounter.

In the classical evolutionary game theory, it is usually assumed that the fitness is determined by the average payoff obtained in consecutive independent encounters. This means that the fitness of an individual becomes linear both with respect to the strategy of the resident population and with respect to the strategy of the individual. This linearity results in some rather unrealistic features as indicated, for example by the Bishop and Cannings (1978) theorem (see, e.g., Meszéna et al. (2001)). Moreover, even though evolutionary game theory considers the frequencies of different strategies, it omits the overall population density. This is a major drawback, especially when considering long-term evolution (Heino et al., 1998).

3.2 The adaptive dynamics approach

Adaptive dynamics (Metz et al., 1992, 1996; Dieckmann and Law, 1996; Geritz et al., 1997, 1998) is a tool for studying the course of frequency- and density-dependent evolution of continuous traits (strategies) in ecological models. The first step in any application of adaptive dynamics is the identification of traits, the evolution of which one is interested in. These traits form the strategy of an individual, and the set of their possible values is the strategy space. In the simplest case, the strategy is one-dimensional, e.g., age at maturation, and the strategy space is some interval on the real line. Below, adaptive dynamics tools are introduced in the case of one-dimensional strategies. The generalization to vector-valued strategies is rather straightforward (Dieckmann and Law, 1996; Matessi and Di Pasquale, 1996; Leimar, 2001, 2005, 2009), but the case of infinite-dimensional (function-valued) strategies requires more care (Dieckmann et al., 2006; Parvinen et al., 2006, 2013). The strategies studied in this thesis are either one- or two-dimensional.

The key idea in adaptive dynamics is to model explicitly the ecological dynamics and to derive the invasion fitness function mechanistically from the life-history of the individuals, whereas most of the other approaches of evolutionary modeling are based on phenomenologically built fitness functions. For the derivation of the invasion fitness function, it is necessary that invasion fitness itself is exactly mathematically defined. This definition was given by Metz et al. (1992) who stated that the invasion fitness of a rare mutant with strategy s^{mut} is its long-term exponential growth rate $r(s^{\text{mut}}, E^{\text{res}})$ in the environment E^{res} set by the residents. If $r < 0$, the mutation will sooner or later vanish from the population. If $r > 0$, the mutant strategy may still be eliminated from the population due to the demographic stochasticity at the initial phase of the invasion, but it may also increase in population density and either coexist with the residents or oust some of the resident strategies.

The derivation of the invasion fitness function and the analysis of the evolutionary dynamics are based on the following three basic assumptions:

1. Clonal reproduction.
2. Rarely occurring mutations allowing the separation of ecological and evolutionary time-scales.
3. Small initial mutant frequency in a large resident population.

In addition, it is usually assumed that:

4. The mutational steps are small, i.e., a new mutant always resembles one of the existing residents.
5. If a mutant can invade a monomorphic resident population, but invasion under reversed roles is not possible, the mutant will replace the resident.
6. If a mutant can invade a monomorphic resident population, but the invasion under reversed roles is also possible, then the resident and the mutant will coexist.

Detailed discussions on the status of these assumptions are given by Geritz et al. (2002), Geritz (2005), Geritz and Gyllenberg (2005) and Meszéna et al. (2005).

Whereas population genetics considers the short-term evolution of allele distributions, the adaptive dynamics analysis usually involves only a limited number of different strategies present in the resident population although the number of possible strategies may be infinite. This limitation allows one, based on the known ecological dynamics, to calculate the population-dynamical attractor of the resident population.

It is possible to formulate almost any reasonable ecological model of population dynamics such that it contains an environmental interaction variable, say E, such that the population dynamics affect this variable, but once its value is known, the equations describing population dynamics are linear (Diekmann et al., 1998, 2001, 2003, 2007). Due to the assumption (2.) of rarely occurring mutations, the resident population is always on the population-dynamical attractor when a new mutant strategy enters the population. On the population-dynamical attractor, the resident sets, together with the abiotic factors, the value of the environmental interaction variable. Let this environment set by the resident population be E^{res}. This variable, E^{res}, may be a scalar, a vector, or even an infinite-dimensional variable. This thesis focuses on discrete-time population models. In such models, it is natural that the biotic factors affecting the environment E^{res} are different for each time unit. The invasion fitness $r(s^{\text{mut}}, E^{\text{res}})$, however, is not determined for any single time unit, but it is the long-term average of the exponential growth rate. Therefore, it is obvious that the variable E^{res} must be of the form $E^{\text{res}} = (E^{\text{res}}(1), E^{\text{res}}(2), \ldots, E^{\text{res}}(n), \ldots)$, where $E^{\text{res}}(n)$ is the environment that determines the growth of the mutant population at time-unit n.

According to the assumption (3.), the mutant population is initially small, and thus, its effect on the environment is negligible. Therefore, at the initial phase of invasion, its population dynamics may be approximated by a linear differential (or difference) equation, where the per capita growth rate of the mutant population determines the invasion fitness of the mutant strategy (Metz et al., 1992). Let now s^{mut} denote the mutant strategy and let $r(s^{\text{mut}}, E^{\text{res}})$ denote the invasion fitness of the mutant in the environment set by the resident.

Assumption (4) is necessary when one wants to deduce the expected direction of evolution based on the local properties of the invasion fitness and local fitness gradient that will be derived below derived on the basis of invasion fitness.

Assumptions (5.) and (6.) allow majority of the evolutionary analysis of ecological models to be built on invasion fitness (Geritz et al., 1998, 2002). In most ecological scenarios, these assumptions follow directly from the previous assumptions when the population-dynamical attractor of the resident population is unique. When there are several possible ecological attractors for the resident population dynamics, the situation is more complicated. Consider, for example, the case in which the resident population has two alternative stable attractors, say A and B. Then the environment set by the resident is not unique, but it is different for each attractor. Denote now the environment set by the resident while on the attractor A by $E^{\text{res}}_{\text{A}}$ and the environment set by the resident while on the attractor B by $E^{\text{res}}_{\text{B}}$. Furthermore, assume that $r(s^{\text{mut}}, E^{\text{res}}_{\text{A}}) > 0$ and

$r(s^{\mathrm{mut}}, E_{\mathrm{B}}^{\mathrm{res}}) < 0$. Now, a mutant that enters while the resident is on the attractor A starts to increase in population density. In most cases, the appearance of the mutant does not cause significant changes in the attractors of the population dynamics even if the mutant ousts the resident (Geritz et al., 2002). Sometimes, however, it is possible that, due to the appearance of the mutant, the population dynamical attractor A becomes unstable, and the population (mutant–resident dynamics) evolves to the alternative attractor B, on which the mutant population starts to diminish and finally dies out. Therefore, the prevalent strategy of the population remains unchanged but the population-dynamical attractor changes qualitatively. This is the so called ”resident strikes back” scenario (Doebeli, 1998; Mylius and Diekmann, 2001; Dercole et al., 2002).

A special extreme case of this scenario is the evolutionary suicide, where the alternative resident attractor B is the trivial attractor that corresponds to extinction. Under certain ecological conditions, it is possible that an invading mutant can oust the resident, even though it is not viable alone. In this case, it is possible that evolution drives the species to extinction, i.e., evolutionary suicide occurs (Matsuda and Abrams, 1994a,b; Ferrière, 2000; Rankin and Lopez-Sepulcre, 2005; Parvinen, 2005, 2007). In the case of a polymorphic population, it is also possible that only one morph is driven to extinction, which may even result in evolutionary branching–extinction cycles (Kisdi et al., 2001; Dercole, 2003; Nurmi and Parvinen, 2013). Evolutionary suicide (evolutionary self-extinction, Darwinian extinction) is possible, since traits that are harmful to the viability of the species may still be beneficial at the individual level, which allows them to become more common in the population (Webb, 2003). This may be related, e.g., to the ”tragedy of commons” (Hardin, 1968).

There are two different types of evolutionary suicide. Mutations that are harmful at the population-level may cause the population size to become extremely small such that the population is finally wiped out by demographic stochasticity (Matsuda and Abrams, 1994a), but it is also possible that the evolutionary suicide occurs fully deterministically (Gyllenberg and Parvinen, 2001; Gyllenberg et al., 2002). Typically, scenarios resulting in deterministic evolutionary suicide involve Allee-effects (Stephens et al., 1999). However, Allee-effects are not the only route to deterministic evolutionary suicide, because it may be enabled also by, e.g., non-equilibrium ecological dynamics (Parvinen, 2005; Nurmi and

Parvinen, 2013).

It is noteworthy that the condition $r(s^{\text{mut}}, E^{\text{res}}) < 0$ implies that the mutant is liable to become ousted from the population, whereas the condition $r(s^{\text{mut}}, E^{\text{res}}) > 0$ only implies that the mutant population is capable to invade the mutant population. However, at the initial phase of an invasion, the invading mutant population only comprises one (or a few) individual(s). Therefore, a mutant, however fit it may be, can vanish from the resident population due to demographic stochasticity. In this case however, the resident population remains unchanged. Thus, a corresponding mutant is liable to later again repeatedly appear in the resident population until it survives the stochastic initial phase of the invasion, and finally invades the resident population.

3.3 The evolutionary analysis of scalar-valued strategies in monomorphic populations

Below, it is assumed that the strategy under consideration is scalar-valued, i.e., one-dimensional. It is also assumed that the resident population is initially monomorphic, i.e., all the resident individuals have the same strategy. However, the generalization of the presented results to polymorphic resident populations is rather straightforward. Furthermore, it is assumed that the population-dynamical attractor of the resident strategy is unique. As mentioned above, this simplifies the evolutionary analysis, since then also the environment E^{res} set by the resident is uniquely determined for each resident strategy, and thus, it is possible to base the evolutionary analysis solely on the invasion fitness, which can be considered as a function of two variables; strategies s^{mut} and s^{res}, of which the latter one acts through the environmental interaction variable E^{res}.

Since the mutational steps are assumed to be small (assumption (4.)), the expected direction of evolution in this monomorphic population is given by the local fitness gradient

$$D(s^{\text{res}}) = \left[\frac{\partial r(s^{\text{mut}}, E^{\text{res}})}{\partial s^{\text{mut}}} \right]_{s^{\text{mut}} = s^{\text{res}}} . \tag{3}$$

Of special interest are the so called singular strategies s^* for which $D(s^*) = 0$, i.e., directional selection vanishes in the monomorphic population. A classification of all possible generic types of singular strategies and their interpretation is given by Metz et al. (1996) and Geritz et al. (1997, 1998). Properties of singular strategies and directions of evolution in a monomorphic population may be analyzed graphically by a pairwise invadability plot, or PIP, (Matsuda, 1985; van Tienderen and de Jong, 1986; Metz et al., 1996; Geritz et al., 1998). PIPs representing the four most important classes of singular strategies are illustrated in Figure 1.

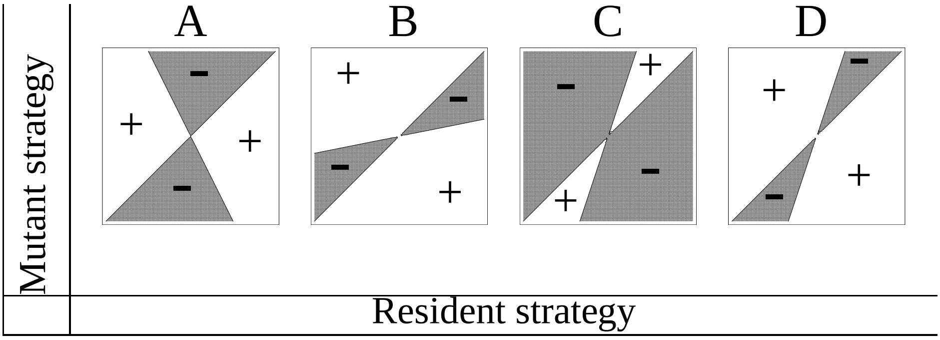

Figure 1: Examples of pairwise invadability plots and qualitatively different singular strategies. In the white areas a mutant strategy may invade the resident population. In the gray areas the invasion is not possible.
Panel A: Evolutionarily attracting and uninvadable singular strategy.
Panel B: Evolutionarily repelling and invadable singular strategy.
Panel C: ”Garden of Eden” evolutionarily repelling singular strategy.
Panel D: Evolutionary branching point.

A pairwise invadability plot is the sign plot of the invasion fitness $r(s^{\text{mut}}, E^{\text{res}})$ such that the horizontal axis corresponds to the set of all possible resident strategies and the vertical axis to the set of all possible mutant strategies. A white point in the PIP indicates that the corresponding mutant strategy can invade a population with the corresponding resident strategy, i.e., $r(s^{\text{mut}}, E^{\text{res}}) > 0$. Correspondingly, a black point indicates that the mutant cannot invade, i.e., $r(s^{\text{mut}}, E^{\text{res}}) < 0$. The curves separating white and black regions in the PIP are the fitness isoclines given by the trait combinations for which $r(s^{\text{mut}}, E^{\text{res}}) = 0$. The main diagonal is trivially such an isocline, since $r(s^{\text{res}}, E^{\text{res}}) = 0$ due to the assumption (2) that ensures that the resident is always on a population-dynamical attractor, and on a population-dynamical attractor, the population does neither grow nor decrease in population size. The configuration of the other, nontrivial, isocline(s) determines the singular strategies and their properties. Singular strategies lie at those points where a nontrivial fitness isocline crosses the diagonal. Even though each PIP in figure 1 has only one singular strategy (s^*), it is possible that the strategy space contains arbitrarily many singular strategies.

Assuming that only mutants slightly different from the resident can occur (assumption (4.)), one can confine the analysis of each PIP to a narrow strip along the diagonal where the mutant and resident strategies are identical. For example, consider the PIP in Figure 1A. From the black-and-white pattern it can be seen that a resident population with an arbitrary strategy s such that $s < s^*$ can be invaded by mutants with a slightly larger strategy but not by mutants with a slightly smaller strategy. The opposite is true for a resident population with any strategy $s > s^*$. In this sense, the strategy s^* is evolutionarily attracting. Moreover, it can also be seen that a resident population with strategy $s = s^*$ cannot be invaded by any nearby mutant, and therefore it is uninvadable, i.e., evolutionarily stable strategy (ESS, Maynard Smith and Price (1973)).

The singular strategy in the figure 1B has the opposite properties. It is evolutionarily repelling and, moreover, can be invaded by any nearby mutant. The singular strategy in figure 1C represents so called ”Garden of Eden” configuration: It is evolutionarily stable in the sense, that once the resident population has exactly the singular strategy s^*, it is uninvadable by any nearby mutant. However, the singular strategy is not evolutionarily attracting, and therefore, any slightest deviation makes the population to evolve away from the neighborhood of the singular strategy. In natural systems, such deviations are unavoidable, and thus in practice, there is no need to distinguish invadable and uninvadable singular strategies whenever they are evolutionarily repelling.

The singular strategy in figure 1D is evolutionarily attracting but invadable. A singular strategy of this type is called an evolutionary branching point. In the neighborhood of an evolutionary branching point, there exists a domain of strategies that can coexist in a protected dimorphism in the ecological time-scale. Consider now two strategies, say x and y. Let E^x (or E^y) be the environment determined by a monomorphic resident population with strategy x (or y). Strategies x and y can coexist in a protected dimorphism if both $r(x, E^y)$ and $r(y, E^x)$ are positive. This means that if, in this coexistence, one of the two strategies would be rare, it would grow in population size since the environment would be, practically, set by the competing strategy.

The existence of strategy pairs capable for such protected coexistence can be identified from pairwise invadability plots by switching the roles of the mutant and resident strategy (mirroring with respect to the diagonal) and placing the resulting PIP on top of each other with the original PIP. Altogether, close to the branching point, the population becomes dimorphic. When the population is dimorphic in the neighborhood of an evolutionary branching point, it can be invaded only by mutants that are further away from the branching point. Thus, the population encounters divergent selection and, on each successive invasion, the two resident strategies become, at least initially, more and more distinct from each other (Metz et al., 1996; Geritz et al., 1997, 1998, 2004).

Whenever evolutionary branching is considered, the basic assumption (1) of clonal reproduction becomes crucial. Kisdi and Geritz (1999) have shown that clonal adaptive dynamics can for large extent predict the course of evolution in monomorphic diploid sexually reproducing populations as well. In the case of branching points, however, the clonal adaptive dynamics predicts that the strategy of a monomorphic population evolves towards the neighborhood of the branching point where disruptive selection promotes ecological diversification. The same is true also for monomorphic sexually reproducing populations. What happens under the influence of such disruptive selection, depends on the genetical architecture and the mating system of the species (Dieckmann and Doebeli, 1999; Geritz and Kisdi, 2000; van Doorn and Weissing, 2001). In clonally reproducing populations, diversification splits the population to two distinct lineages that encounter divergent evolution, which makes their strategies to evolve further away from each other. In diploid populations, however, this split is prevented by the averaging effect of sexual reproduction, unless some form of assortative mating evolves (see, e.g., van Doorn and Dieckmann (2006); van Doorn et al. (2009); Ripa (2009); Kisdi and Priklopil (2011)). Altogether, the mere existence of an evolutionary branching point does not lead to ecological speciation. Branching points can only indicate ecological circumstances that may promote diversification which may, if mating barriers evolve, result in speciation.

Besides the properties introduced in Figure 1, the isocline configurations in pairwise invadability plots may differ qualitatively in the ability of the singular strategy to invade other strategies in its neighborhood. However, this property is of interest only in the case of an evolutionarily attracting ESS, and even then the interest is minor, since this property only determines the way the ESS is approached. If the ESS can invade neighborhood strategies, it is possible, that the population ends up exactly to the ESS in a discrete step. In the opposite case, population can only approach the ESS as a limit process that may be restricted by the minimum size of possible mutations, which is usually assumed to exist in the adaptive dynamics analysis.

If the mutations were infinitesimally small, evolutionary analysis based on dynamical systems theory would be possible using the canonical equation of adaptive dynamics (Dieckmann and Law, 1996; Champagnat et al., 2001, 2006, 2008; Durinx et al., 2008). Thus, the existence of the minimum size of possible mutations together with mutational stochasticity separates adaptive dynamics approach from standart dynamical systems theory and enables, e.g., the analysis of evolutionary branching, which increases the dimensionality of the evolving system and is therefore outside the scope of the dynamical systems theory as such.

When selection is both frequency- and density-dependent, the invadability and the evolutionary attractivity of a singular strategy are independent of each other, whereas in optimization models (fitness landscapes) and game-theoretical models they are contingent on each other (Meszéna et al., 2001; Dieckmann and Metz, 2006). This, together with the game-theoretical history of adaptive dynamics, has caused some variation and inconsistency in the terminology used by different authors. The term ESS (evolutionarily stable strategy) (Maynard Smith and Price, 1973), that refers to strategies that cannot be invaded by any nearby strategy, is nowadays well established, even though the established interpretation is rather misleading from the point of view of the traditional theory of dynamical systems, where an equilibrium point in a state-space is stable if the state of the system converges to this point whenever the initial state is close enough to this point (Devaney, 1989; Verhulst, 1996). However in adaptive dynamics, evolution starting from a neighborhood of an ESS that is not evolutionarily attracting will direct away from the ESS. In Figure 1, both cases A and C illustrate evolutionarily stable (uninvadable) strategies even though only the singular strategy illustrated in panel A would be stable in the terminology of dynamical systems. Moreover, evolutionarily attracting strategies are also called convergence stable strategies (Christiansen, 1991). Furthermore, Eshel and coworkers use the term continuously stable strategy (CSS) for a convergence stable ESS (Eshel and Motro, 1981; Eshel, 1983; Eshel et al., 1997).

The pairwise invadability plots (figure 1) allow the graphical analysis of the global evolutionary attractivity and global invadability of singular strategies. However, due to assumption 4 of small mutational steps, even local evolutionary attractivity and invadability are sufficient for evolutionary analysis. The local properties of the singular strategies may be analyzed also algebraically based on the values of the second order partial derivatives of the function $r(s^{\text{mut}}, E^{\text{res}})$ (Geritz et al., 1998). Let now s^* be a singular strategy, i.e.,

$$D(s^*) = \left[\frac{\partial r(s^{\text{mut}}, E^{\text{res}})}{\partial s^{\text{mut}}}\right]_{s^{\text{mut}}=s^{\text{res}}=s^*} = 0.$$

If s^* is a local fitness maximum in the environment set by the strategy s^*, i.e.,

$$\left[\frac{\partial^2 r(s^{\text{mut}}, E^{\text{res}})}{(\partial s^{\text{mut}})^2}\right]_{s^{\text{mut}}=s^{\text{res}}=s^*} < 0,$$

then s^* is a locally uninvadable strategy (compare to Figure 1A). Similarly, if this second order partial derivative is negative, then s^* is a fitness minimum in the environment set by the strategy s^* Thus, it can be invaded by any nearby strategy, which means that it is a branching point (compare to Figure 1D). Monomorphic evolution to such fitness minimums is possible since, under frequency-dependent selection, each resident strategy s^{res} determines different environment E^{res} where fitness landscape experienced by a mutant with strategy s^{mut}, i.e, $r(s^{\text{mut}}, E^{\text{res}})$ considered as a function of the mutant strategy s^{mut}, determines which mutants may invade the resident population. However, once a mutant invades and replaces the resident, it determines a new, different, fitness landscape. Figure 2 illustrates the way this process may lead either to a (local) fitness maximum or to a (local) fitness minimum.

In monomorphic populations, the expected direction of evolution is given by the sign of the local fitness gradient $D(s)$ (see equation 3). For singular strategies s^* , the fitness gradient $D(s^*) = 0$. Furthermore, the

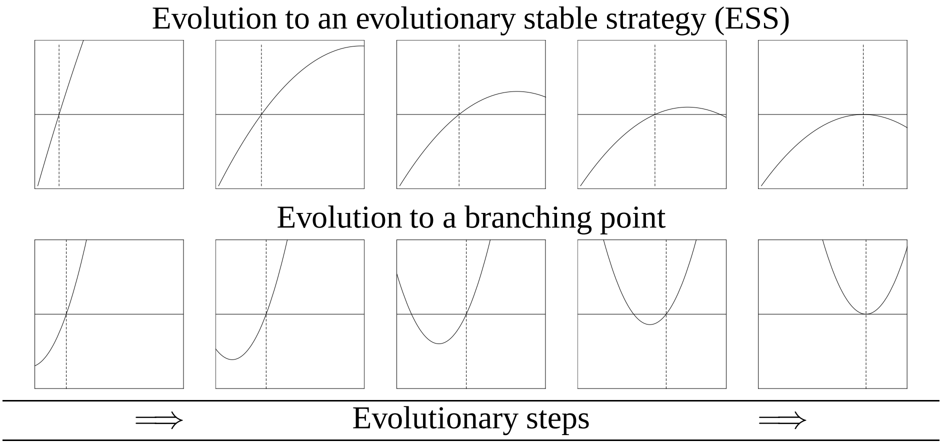

Figure 2: In each panel, the invasion fitness $r(s^{\text{mut}}, E^{\text{res}})$ (vertical axis) is plotted with respect to the mutant strategy s^{mut} (horizontal axis) in the environment set by a monomorphic resident population with the strategy s^{res} indicated by the vertical dashed line. In each panel, next evolutionary step will be towards right, i.e., the resident strategy s^{res} is replaced with a mutant strategy s^{mut} such that $s^{\text{mut}} > s^{\text{res}}$, until, in the rightmost panel, a singular strategy is reached. On the upper row, this singular strategy is a local fitness maximum, i.e., an ESS, and on the lower row, the singular strategy is a local fitness minimum, i.e., a branching point.

sign of the fitness gradient in the neighborhood of s^* can be deduced from $D'(s^*)$. Thus, the singular strategy is evolutionarily attracting, if $D'(s^*) < 0$, and repelling if $D'(s^*) > 0$. Furthermore, the value of $D'(s^*)$ can be calculated as

$$D'(s^*) = \left[\frac{\partial^2 r(s^{\text{mut}}, E^{\text{res}})}{(\partial s^{\text{mut}})^2} - \frac{\partial^2 r(s^{\text{mut}}, E^{\text{res}})}{(\partial s^{\text{res}})^2} \right]_{s^{\text{mut}}=s^{\text{res}}=s^*} .$$

Moreover, if

$$\left[\frac{\partial^2 r(s^{\text{mut}}, E^{\text{res}})}{(\partial s^{\text{res}})^2} \right]_{s^{\text{mut}}=s^{\text{res}}=s^*}$$

is positive, then s^* can invade neighborhood strategies. If any of these expressions vanishes, the properties of the singular strategies must be deduced from higher order partial derivatives (based on Taylor-series expression of the invasion fitness function).

3.4 Evolutionary analysis of scalar-valued strategies in polymorphic populations

So far, only monomorphic populations have been considered. The adaptive dynamics approach, however, applies to di- or polymorphic populations as well. The algebraic tools provided by adaptive dynamics are applicable, given that it is possible to find the attractor of the ecological dynamics, be it an equilibrium or a periodic orbit. Even when the population-dynamical attractor cannot be found algebraically, adaptive dynamics tools may still enable evolutionary analysis. If a stable population-dynamical attractor exists, it can often be found by iterating the ecological population dynamics sufficiently long. Once the attractor has been found with numerical methods, the theoretical methods provided by adaptive dynamics apply for evolutionary analysis.

Furthermore, the adaptive dynamics approach allows efficient evolutionary simulations since the ecological model for the population dynamics is specified, and thus, resource-consuming individual-based simulations can be replaced with simulations that are built on the iteration of the ecological dynamics of a polymorphic population together with infrequent insertions of new mutants, and removals of strategies that have become rare enough to be considered extinct. In this thesis, all these tools are being used: algebraic analysis, numerical analysis and simulations based on iteration of ecological dynamics with rare randomly occurring mutations.

3.5 Joint evolution of several traits (vector-valued strategies)

One of the main topics of this thesis is to show that the joint evolution of specialization and dispersal propensity may allow an initially monomorphic population to become trimorphic such that a generalist morph coexists with two specialist morphs. Studying the joint evolution of two traits means that one has to consider vector-valued traits. Leimar (2001, 2005, 2009) has shown that, in this case, different mutational variance–covariance structures and fitness interactions may crucially affect the evolutionary dynamics.

In the case of one-dimensional traits and small mutations, the evolutionary dynamics are rather simple: if the fitness gradient $D(s^{\mathrm{res}})$ is positive, only mutants with higher trait value may invade the resident strategy s^{res}, and the evolutionary path is qualitatively similar for any sequence of successive mutations. In the case of two co-evolving traits, there are usually at least two qualitatively different types of mutants that may invade the resident strategy.

Consider, for example, the joint evolution of dispersal propensity and specialization. Then, in the absence of pleiotropy, the resident population may be invaded either by mutants that differ only in the dispersal propensity or by the mutants that differ only in the specialization strategy. Even in this non-pleiotropic case the order of stochastic mutation events may significantly affect the outcomes of evolution, and the evolutionary dynamics are not, even qualitatively, independent of the mutation process (Nurmi and Parvinen, 2011).

If pleiotropic mutations affecting simultaneously both the dispersal propensity and specialization are possible, the set of mutant strategies capable of invading the resident is notably larger. Furthermore, there may be fitness interactions such that the sign of the invasion fitness of a pleiotropic mutant cannot be deduced from the invasion fitnesses of the non-pleiotropic mutants. For example in the case of joint evolution of dispersal propensity and specialization, biological intuition might let one to expect that a mutant that is simultaneously both more specialized and less dispersive might be able to invade a resident strategy that is uninvadable against both strategies that differ only in the specialization strategy and strategies that differ only in the dispersal propensity.

In this thesis, as well as in the analysis committed by Nurmi and Parvinen (2011) pleiotropic mutations are assumed to be impossible. Since even non-pleiotropic mutations are sufficient to enable the evolution to the trimorphic coexistence of specialists and generalists, it is not necessary to add in the full complexity of pleiotropic mutations even though they may sometimes enable the emergence of additional biodiversity.

4 Mechanistic derivation of ecological models for the adaptive dynamics of resource use

The agenda of this section is to show how to derive metapopulation models that are suitable for the evolutionary analysis of resource usage. As mentioned above, this process has to start from the individual level; here the starting point is a continuous-time resource-consumer model with two alternative resources. Geritz and Kisdi (2004) have shown that a simple argument of time-scale separation allows one to derive from this model a discrete-time model for the consumer population. Once the discrete-time consumer population dynamics have been specified in a single well-mixed population, lifting this model to the metapopulation level is just a question of book-keeping, as has been shown by, e.g., Gyllenberg et al. (1997) and Parvinen (2006).

The model derivation is followed by the derivation of the invasion fitness function in these models. In order to calculate invasion fitness in metapopulations, it is necessary to understand the calculation of invasion fitness for well-mixed populations. Therefore, both of the calculations will be presented here.

4.1 Discrete-time model for local population dynamics

The derivation of a discrete-time model for the well-mixed population is based on the guidelines given by Geritz and Kisdi (2004). Their approach applies to species that hatch at the beginning of season, use resources from the environment to produce new eggs that also encounter mortality during the breeding season. At the end of the breeding season, all of the adults die and only a fraction of the eggs survives to the following season. The other eggs are lost. For simplicity, it is also assumed that there is no within-season mortality among the adults.

In the modeling technique of Geritz and Kisdi (2004), the details of the continuous-time resource-dynamics determine the type of the discrete-time consumer-dynamics. Below, the model derivation is presented in the case of general resource-growth functions and a monomorphic consumer population (all the consumers are identical). Later, the model is generalized to the case of several consumer types, and specific resource-growth functions are introduced in order to derive some well-known discrete-time population models.

First, let the variables $n \in \mathbb{N}$ and $t \in [0, 1]$ denote two different measures of time such that the discrete variable n determines the number of year (or breeding season) whereas the continuous variable t determines time within that season. Let now $A_n^{(i)}(t)$ be the availability of the resource i at time t during season n, and let $\alpha_i G_i(A_i)$ be the density-dependent per capita growth rate of the resource i, where G_i is assumed to be a decreasing function.

Then the within-season continuous-time resource dynamics, in the absence of consumers, are

$$\frac{dA_n^{(i)}}{dt}(t) = \alpha_i G_i\big(A_n^{(i)}(t)\big)A_n^{(i)}(t). \tag{4}$$

Assume now, that the resources are used by a monomorphic consumer population with population density x_n during the breeding season n. The consumer population size x_n is constant since it is assumed that the consumers do not encounter within-season mortality, but they all perish at the end of the breeding season. Assume further that consumers use the resource i according to the law of mass-action with the rate β_i, and the consumed resources are converted to new eggs with efficiency γ_i. Now, let the density of the eggs of the consumer at time t during season n be $U_n(t)$ and assume that, during breeding season, the already oviposited eggs are destroyed with rate δ. The eggs are identical, independent of the resource usage of the consumer who produced the egg.

With these assumptions, it is possible to formulate the within-season dynamics for a monomorphic consumer population as

$$\begin{aligned} \varepsilon\frac{dA_n^{(i)}}{dt}(t) &= \alpha_i G_i\big(A_n^{(i)}(t)\big)A_n^{(i)}(t) - \beta_i A_n^{(i)}(t)x_n \\ \frac{dU_n}{dt}(t) &= \big(\gamma_1\beta_1 A_n^{(1)}(t) + \gamma_2\beta_2 A_n^{(2)}(t)\big)\, x_n - \delta U_n(t), \end{aligned} \tag{5}$$

where ε is a small dimensionless scalar that allows one to assume that the resource dynamics are fast enough (compared to consumer egg dynamics) in order to assume that the resource densities are always at the stable quasi-equilibrium value set by the current consumer population density x_n. This value,

$$\widehat{A}_n^{(i)} = \max\left\{0, G_i^{-1}\left(\frac{\beta_i}{\alpha_i}x_n\right)\right\}, \tag{6}$$

can be interpreted as the availability of the resource i during season n. For some resource-growth functions, high consumer density may result in negative values of $G_i^{-1}\left(\frac{\beta_i}{\alpha_i}x_n\right)$. In these cases, the resource availability diminishes (rapidly) until the resource has become completely absent (exhausted), which means that this resource cannot be used for egg production. Once a resource is exhausted, devoted specialists, utilizing solely this resource, cannot produce any eggs, and thus perish over the winter. If both resources are exhausted simultaneously, none of the consumers can produce any eggs, which means that once the adult consumers die at the end of the season, the entire population has perished. The exhausted resource recovers at the beginning of the next breeding season given that the consumer population has diminished sufficiently.

Now, the egg density obeys the linear differential equation,

$$\frac{dU_n}{dt}(t) = \left(\gamma_1\beta_1\widehat{A}_n^{(1)} + \gamma_2\beta_2\widehat{A}_n^{(2)}\right)x_n - \delta U_n(t). \tag{7}$$

It is easy to find the solution of this equation:

$$U_n(1) = \frac{1-e^{-\delta}}{\delta}\left(\gamma_1\beta_1\widehat{A}_n^{(1)} + \gamma_2\beta_2\widehat{A}_n^{(2)}\right)x_n.$$

Now, assuming further that fraction σ_i of these eggs survives to next season and hatches successfully, one can calculate

$$x_{n+1} = \sigma_i U_n(1).$$

It is now possible to simplify the notation by defining a new compound parameter

$$\lambda_i = \frac{\sigma_i\gamma_i}{\delta}(1-\exp(-\delta)).$$

With this notation, one can write down the discrete-time model for the consumer population as

$$x_{n+1} = \sum_{i=1}^{2}\lambda_i x_n \beta_i \widehat{A}_n^{(i)}. \tag{8}$$

Next, consider the case of several consumers that are identical except for the resource consumption rates β. Let j denote the consumer type and let $x_n^{(j)}$ be the type j consumer population density during the breeding season n. Assume also that the type j consumers use the resource i according to the law of mass action with rate β_{ij}. Furthermore, assume that the other parameters in the resource–consumer model (5) are independent of the consumer type. Then the resource dynamics for type i resource become

$$\varepsilon \frac{dA_n^{(i)}}{dt}(t) = \alpha_i G_i\big(A_n^{(i)}(t)\big) A_n^{(i)}(t) - A_n^{(i)}(t) \sum_m \beta_{im} x_n^{(m)}.$$

As above, it is possible to solve the quasi-equilibrium resource density

$$\widehat{A}_n^{(i)} = \max\left\{0, G_i^{-1}\left(\frac{\sum_m \beta_{im} x_n^{(m)}}{\alpha_i}\right)\right\}. \tag{9}$$

Once this value is known, the differential equation determining the egg dynamics is the same as above (equation 7) and one obtains a general discrete-time model with two resources for several consumers:

$$x_{n+1}^{(j)} = \sum_{i=1}^{2} \lambda_i \beta_{ij} \widehat{A}_n^{(i)} x_n^{(j)}. \tag{10}$$

In this equation, λ_i is a resource-specific parameter, and β_{ij} depends on the consumer strategies but not on the consumer population sizes. Thus at the level of ecological dynamics, they are constant parameters. Therefore, if the resource availabilities $\widehat{A}_n^{(1)}$ and $\widehat{A}_n^{(2)}$ are known, the ecological dynamics (equation 10) are linear. Thus at time unit n, the environment set by competing residents is determined by the resource availabilities, i.e.,

$$E^{\text{res}}(n) = \begin{pmatrix} \widehat{A}_n^{(1)} \\ \widehat{A}_n^{(2)} \end{pmatrix}. \tag{11}$$

If one now defines the fecundity function of type j consumers with strategy s^j as

$$f(s^j, E^{\text{res}}(n)) = \Big(\lambda_1 \beta_{1j} \widehat{A}_n^{(1)} + \lambda_2 \beta_{2j} \widehat{A}_n^{(2)}\Big), \tag{12}$$

then the population model (10) can be written in the form

$$x_{n+1}^{(j)} = f(s^j, E^{\text{res}}(n))x_n^{(j)}. \tag{13}$$

In order to illuminate the differences between generalists and specialists, the resources are, in this thesis, assumed to be equivalent both in nutritional values and in renewal rates, but possibly different in availabilities, i.e., $\alpha_1 = \alpha_2 = \alpha$, $\lambda_1 = \lambda_2 = \lambda$, but K_1 can be different from K_2.

This mechanistically underpinned population model is, in slightly different forms (based on different resource growth functions), widely utilized and analyzed in the articles 2, 3 and 4, in which it is generally assumed, that the resource growth rate has been scaled such that $\alpha = 1$. However, in article 1 a different modeling approach is assumed in order to create a model which is equivalent to the models of habitat specialization and habitat selection, but which underpins the differences between habitats by varying resource availabilities.

Below, three different resource-growth functions and the three different resulting discrete-time consumer population models are introduced.

The Beverton–Holt model

Let now the resources to have chemostat dynamics such that the internal within-season growth rate of the resource population i equals α and carrying capacity of the resource equals K_i. Then the resource dynamics in the absence of consumers (equation 4) are

$$\frac{dA_n^{(i)}}{dt}(t) = \alpha G\big(A_n^{(i)}(t)\big)A_n^{(i)}(t) = \alpha\left(1 - \frac{A_n^{(i)}(t)}{K_i}\right), \tag{14}$$

This equation can be equally interpreted such that there is a constant influx of the resource to the system with rate α and the resources decay exponentially with rate $\frac{\alpha}{K_i}$. In this case (see equation 6),

$$G_i(A) = \left(\frac{1}{A} - \frac{1}{K_i}\right) \qquad \text{and} \qquad G_i^{-1}(x) = \frac{1}{\frac{1}{K_i} + x}.$$

The inverse function G_i^{-1} is always positive, which means that the quasi-equilibrium resource density in the case of several consumers (equation

9) can be written as

$$\widehat{A}_n^{(i)} = \frac{\alpha}{\frac{\alpha}{K_i} + \sum_m \beta_{im} x_n^{(m)}}, \tag{15}$$

and the between-season consumer dynamics (equation 10), with $\alpha = 1$, obey the difference equation

$$x_{n+1}^{(j)} = \lambda x_n^{(j)} \left(\frac{\beta_{1j} K_1}{1 + \sum_m K_1 \beta_{1m} x_n^{(m)}} \right) + \lambda x_n^{(j)} \left(\frac{\beta_{2j} K_2}{1 + \sum_m K_2 \beta_{2m} x_n^{(m)}} \right), \tag{16}$$

which, in the case of one resource and one consumer, is the famous Beverton and Holt (1957) model

$$x_{n+1} = \frac{\lambda \beta K x_n}{1 + \beta K x_n}.$$

The discrete-time logistic model

Assume that the resources have logistic dynamics in the absence of consumers (see equation 4), i.e.,

$$\frac{dA_n^{(i)}}{dt}(t) = \alpha \left(1 - \frac{A_n^{(i)}(t)}{K_i} \right) A_n^{(i)}(t) = \alpha G_i\big(A_n^{(i)}(t)\big) A_n^{(i)}(t),$$

which means that (see equation 6)

$$G_i(A) = \left(1 - \frac{A}{K_i} \right) \qquad \text{and} \qquad G_i^{-1}(x) = K_i(1 - x),$$

of which the latter one is negative for large values of x.

Then, the quasi-equilibrium resource densities (equation 9) are

$$\widehat{A}_n^{(i)} = \max \left\{ 0, K_i \left(1 - \frac{1}{\alpha} \sum_m \beta_{im} x_n^{(m)} \right) \right\}. \tag{17}$$

This means that, if the consumer population becomes overly large, a resource may be exhausted. An exhausted resource cannot be used to the production of new eggs. If both of the resources are exhausted simultaneously, the consumer population cannot produce any eggs, and thus perishes over the winter. Once exhausted, the resource population is assumed to recover immediately at the beginning of the following season.

Altogether, one now obtains a version of the truncated discrete-time logistic model (May, 1976) for the consumer population (with $\alpha = 1$):

$$\begin{aligned} x_{n+1}^{(j)} = \lambda K_1 x_n^{(j)} \beta_{1j} \max\left\{0, \left(1 - \sum_m \beta_{1m} x_n^{(m)}\right)\right\} \\ + \lambda K_2 x_n^{(j)} \beta_{2j} \max\left\{0, \left(1 - \sum_m \beta_{2m} x_n^{(m)}\right)\right\}. \end{aligned} \tag{18}$$

The Ricker model

Assume that the resource dynamics (equation 4) are, in the absence of consumers, given by the Gompertz (1825) equation

$$\frac{dA_n^{(i)}}{dt} = \alpha \mathrm{Ln}\left(\frac{K_i}{A_n^{(i)}(t)}\right) A_n^{(i)}(t) = \alpha G_i\big(A_n^{(i)}(t)\big) A_n^{(i)}(t),$$

which means that

$$G_i(A) = \mathrm{Ln}\left(\frac{K_i}{A}\right) \qquad \text{and} \qquad G_i^{-1}(x) = K_i \exp(-x).$$

As in the case with the Beverton–Holt model (equation 16), the inverse function is again always positive, and the quasi-equilibrium resource densities (equation 9) can be written as

$$\widehat{A}_n^{(i)} = K_i \exp\left(-\frac{\sum_m \beta_{im} x_n^{(m)}}{\alpha}\right).$$

Thus, one obtains the famous Ricker (1954) model that, in the case of two resources and several consumer types (and $\alpha = 1$), has the form

$$\begin{aligned} x_{n+1}^{(j)} =& \lambda K_1 \beta_{1j} x_n^{(j)} \exp\left(-\sum_m \beta_{1m} x_n^{(m)}\right) \\ &+ \lambda K_2 \beta_{2j} x_n^{(j)} \exp\left(-\sum_m \beta_{2m} x_n^{(m)}\right). \end{aligned} \tag{19}$$

4.2 Trade-off between the resource consumption rates

In the population models derived above, the resource usage of type j consumers is determined by two consumption rates: β_{1j} and β_{2j}. It is characteristic to the above models that the dynamics of the resources interact only via shared consumers and, above all, consumers interact only via resource availabilities: the more there are consumers around, and the more efficiently they use resources, the lower are the quasi-equilibrium values $\widehat{A}_n^{(i)}$ of the resource densities, and the more efficient the consumers have to be in using these resources in order to maintain viability. Moreover in these population models, increasing usage rates of the resources do not involve any additional costs, such as increasing exposure to predation. Thus, if resource consumption rates β_{1j} and β_{2j} were to evolve freely without any limitation, these rates would most likely encounter evolution towards ever increasing values. Therefore, there is an obvious need for externally determined limits for these rates, which is typical for all kinds of specialization evolution, whereas for example, the evolution of dispersal (as well as that of reproduction timing) takes place in the balance of inherent costs and benefits of dispersal: dispersal is necessary for long-term survival of the species, but overly abundant dispersal causes unnecessary risks and consumes resources.

Usually in evolution of specialization literature, as well as in this thesis, it is assumed that the growth of the resource consumption rates is limited by a trade-off curve. Below this curve, mutations increasing both of the consumption rates are possible, which means that, in the evolutionary process, the trade-off curve is reached rapidly. Thus on evolutionary analysis, one can focus solely on the evolution along the trade-off curve. (See figure 3B for examples of trade-off curves). On this curve, the better an individual is in utilizing one resource, the worse it is in utilizing the other, and any mutation increasing the consumption rate of one resource must cause a decrease in the consumption rate of the other.

Assume now that the resource consumption rates are determined by the strategy $s \in [0,1]$ of an individual. Assume also that the resource consumption is symmetric in the sense that there exists a function β such that, for type j individuals with strategy s, one can determine $\beta_{1j} = \beta(s)$ and $\beta_{2j} = \beta(1-s)$. In other words, strategy s individuals use resource 1 with rate $\beta(s)$ and resource 2 with rate $\beta(1-s)$ (according to the law of mass-action). In algebraic analysis, the following assumptions are made:

1. Function β is strictly increasing, i.e., the more specialized an individual is on a specific resource, the more efficiently the individual can use this resource.

2. If nothing is invested to the use of a certain resource, nothing is obtained from this resource, i.e., $\beta(0) = 0$.

Since in population-dynamical equations, the function β occurs always as a product with resource carrying capacities, fixing the maximum value of β is just a matter of scaling these parameters appropriately, and one can without loss of generality assume $\beta(1) = 1$. Now, the case $s = 0$ corresponds to a devoted specialist using only resource 2, and the case $s = 1$ to a devoted specialist using only resource 1. The case $s = 0.5$ corresponds to an unbiased generalist.

In numerical explorations, it is necessary to fix the functional form of the resource consumption function (the trade-off curve). In these cases, it is assumed that

$$\beta(s) = \frac{1 - e^{-\theta s}}{1 - e^{-\theta}}, \qquad \theta \neq 0. \tag{20}$$

This formula is not defined for $\theta = 0$, but since $\lim_{\theta \to 0} \beta(s) = s$ it is natural to define $\beta(s) = s$ when $\theta = 0$. This trade-off function in illustrated in Figure 3.

The trade-off parameter θ determines whether the resource consumption function β is convex ($\theta < 0$), concave ($\theta > 0$), or linear ($\theta = 0$). In the case of concave resource consumption function, the resource consumption function increases deceleratingly. This case is sometimes referred as the case of weak trade-off since a generalist can use resources more efficiently than a linear combination of the two specialists, i.e.,

$$\beta(0.5) > \frac{\beta(0) + \beta(1)}{2}.$$

Analogously, in the case of convex resource consumption function, the resource consumption function increases acceleratingly, i.e.,

$$\beta(0.5) < \frac{\beta(0) + \beta(1)}{2},$$

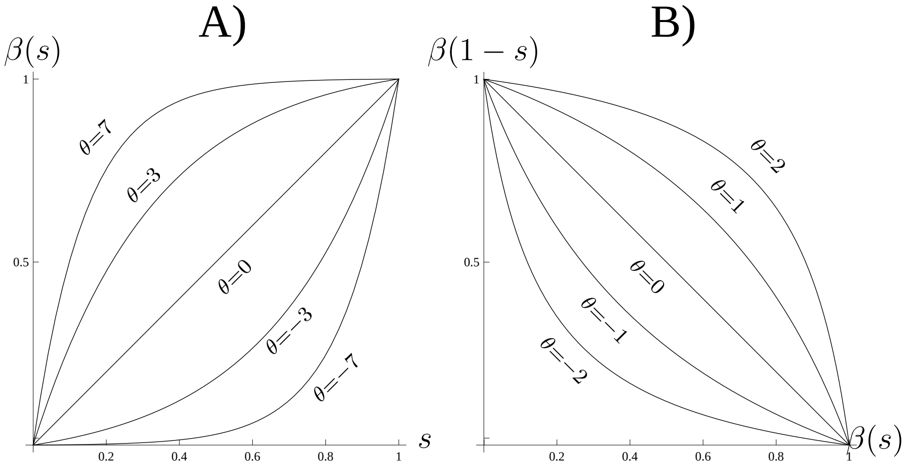

Figure 3: Trade-off curves.
Panel A: Resource consumption rate $\beta(s)$ as a function of the specialization strategy s for different values of the trade-off parameter θ.
Panel B: Consumption rate of resource 2 $\big(\beta(1-s)\big)$ as a function of the consumption rate of resource 1 $\big(\beta(s)\big)$, i.e., the curves delimiting fitness sets in the spirit of Levins (1962, 1963).

which can be interpreted as strong trade-off. In the terminology used by, e.g., White et al. (2006) and Hoyle et al. (2008, 2011), the case of concave resource consumption function corresponds to a trade-off with accelerating costs, and the case of convex resource consumption function corresponds to a trade-off with decelerating costs.

The resource consumption function is the only ingredient in the model presented here that has no mechanistic interpretation. Negative values of θ are used to model phenomenologically the situations in which there is an additional cost of generalism (or switching cost), whereas positive values of θ correspond to cases in which there is an additional benefit of generalism (switching benefit). The linear resource consumption function ($\beta(s) = s,\ \theta = 0$) is an important special case since it can be interpreted, for example, as the search time allocation between the two resources.

In the literature considering the evolution of specialization, an assumption that corresponds to assuming $\beta(s) = s^{\nu}$, where $\nu > 0,$ is rather usual (see, e.g., Egas et al. (2004); Rueffler et al. (2007); Débarre and Gandon (2010) and Zu et al., (2011a)). However in the model described above, this formulation would result in

$$\lim_{\widehat{s}\to 0}\left[\frac{d\beta(s)}{ds}\right]_{s=\widehat{s}} = \infty \quad \text{and} \quad \lim_{\widehat{s}\to 1}\left[\frac{d\beta(1-s)}{ds}\right]_{s=\widehat{s}} = \infty, \quad \text{if } 0 < \nu < 1,$$

$$\lim_{\widehat{s}\to 0}\left[\frac{d\beta(s)}{ds}\right]_{s=\widehat{s}} = 0 \quad \text{and} \quad \lim_{\widehat{s}\to 1}\left[\frac{d\beta(1-s)}{ds}\right]_{s=\widehat{s}} = 0, \quad \text{if } \nu > 1,$$

which may generate artificial singularities extremely near to the borders of the strategy space. With the formulation (20), one obtains resource consumption functions that resemble the case of $\beta(s) = s^{\nu}$, but avoids these artificial singularities.

The family of resource consumption functions given by equation (20) covers a wide range of qualitatively different ecological scenarios. However, the functions in this family are always either everywhere concave or everywhere convex. Hence, e.g., the cases with sigmoidal trade-offs cannot be covered. There are, however, methods in the adaptive dynamics toolbox that are independent of the particular shape of the trade-off function (de Mazancourt and Dieckmann, 2004; Bowers et al., 2005; Kisdi, 2006; Geritz et al., 2007; Kisdi, 2014). These methods can, for example, reveal ecological scenarios where evolutionary branching may occur. From the point of view of evolution of specialization, it would be useful to further develop these methods such that they could be used to reveal or exclude the possibility of the trimorphic coexistence of one generalist strategy with two different specialist strategies in the case of two resources.

4.3 Metapopulation dynamics

Once the local dynamics are derived from the individual level processes (section 4.1), one can build a structured metapopulation model based on this local population model. Below the required assumptions and model derivation are introduced in detail.

It is assumed that the landscape consists of an infinite number of large local habitat patches that are prone to local catastrophes. However, there is only a finite number of different patch types. Each patch can support a local population. Patch types differ from each other only in the carrying capacities of the two resources. In an individual patch, the local population growth rate (fecundity) at time n is set by the resource availabilities at that time. These availabilities are determined by the local population sizes, specialization strategies of the consumers and the local resource carrying capacities as explained in equation (9).

In equation (11) these availabilities were used to determine the environment $E^{\text{res}}(n)$ set by the resident at time-unit n. In metapopulations, however, the environment set by the resident population is determined at the metapopulation level. Instead, the local resource availabilities determine $E^{\text{res}}_{\text{loc}}(n)$ the local environment set by the current local resident population at time n, equally with the definition 11.

Now, in the absence of dispersal and catastrophes, one can write the local dynamics of type j consumers with strategy $s^{(j)}$ in a patch of type m in the form (compare with equation (13))

$$x^{(j)}_{n+1} = f^m\Big(s^{(j)}, E^{\text{res}}_{\text{loc}}(n)\Big)x^{(j)}_n.$$

In fact, once the resource availabilities are known, the fecundity function f^m is identical in all patch types m. However, the notations in the fitness calculations are simpler when differences in the local growth, caused by different resource carrying capacities, are denoted also explicitly in the fecundity function.

Once an individual decides to emigrate, it is assumed to enter the pool of dispersers. The dispersers that survive migration are distributed evenly to all of the patches, independent of their origins. Each individual emigrates with probability e and survives migration with probability π (independent of e). Furthermore, $D_n(s)$ denotes the average number of strategy s dispersers per patch emigrated from the patches at period n (disperser pool size of the strategy s dispersers).

During one time step, a single patch encounters a catastrophe with probability c. These catastrophes occur independently in different patches. When a catastrophe takes place, it wipes out the entire local population. After a catastrophe a new local population is founded by dispersers from the disperser pool. The order of events during a season is assumed to be: Potential catastrophe destroying all the eggs in a patch – hatching – emigration to the disperser pool – immigration from the disperser pool – census – production of the new eggs in the patches.

With these assumptions and notations, the local dynamics of a type j consumer population with strategy $s^{(j)}$ are

$$x_{n+1}^{(j)} = C(n+1)(1-e)f^m\Big(s^{(j)}, E_{\text{loc}}^{\text{res}}(n)\Big)x_n^{(j)} + \pi D_n^{(j)}(s), \tag{21}$$

where $C(n+1)$ is a random variable determining the occurrence of the catastrophes (see equation (2)), and

$$D_n^{(j)}(s) = \sum_m p_m \left(\begin{array}{l} \text{Expected number of strategy } s^{(j)} \text{ emigrants} \\ \text{from a type } m \text{ patch at time } n \end{array} \right). \tag{22}$$

Equations (21) and (22) form the metapopulation model that is analyzed in this thesis.

5 Invasion fitness and environmental interaction variable

5.1 Invasion fitness in well-mixed populations

Consider a k-morphic resident population where the resident strategies are $(s^{(1)}, s^{(2)}, \dots, s^{(k)})$. Suppose that the resident population has settled to an attractor $\left(X_1^{\text{res}}, X_2^{\text{res}}, X_3^{\text{res}}, \dots X_n^{\text{res}}, \dots\right)$, where each X_n^{res} comprises the resident population sizes $(x_n^{(1)}, x_n^{(2)}, \dots, x_n^{(k)})$ at time n. For each n, the local population sizes together with resident strategies and resource carrying capacities determine the environment $E^{\text{res}}(n)$ set by the resident population at time n. Consider now a negligibly small mutant population with strategy s^{mut}. The small mutant population does not affect the environment, and thus based on equation (13), the mutant population dynamics obey the linear difference equation

$$x_{n+1}^{\text{mut}} = f(s^{\text{mut}}, E^{\text{res}}(n))x_n^{\text{mut}}. \tag{23}$$

If, furthermore, the resident population dynamics have settled to a fixed point attractor, then the environment set by the resident remains constant ($E^{\text{res}}(n) = E^{\text{res}}$ for each n), and the equation (23) becomes an autonomous linear difference equation. This means that $f(s^{\text{mut}}, E^{\text{res}})$ is equivalent to the basic reproduction ratio of the mutant population (Diekmann et al., 1990; Heffernan et al., 2005), and one can, in the spirit of Metz et al. (1992), determine the invasion fitness of a rare mutant in the environment set by the residents as (see, e.g., Mylius and Diekmann (1995)).

$$r(s^{\text{mut}}, E^{\text{res}}) = \ln\left(f(s^{\text{mut}}, E^{\text{res}})\right).$$

In principle, the generalization of this invasion fitness function to the case of non-equilibrium dynamics is simple:

$$\begin{aligned} r(s^{\text{mut}}, E^{\text{res}}) &= \lim_{t\to\infty} \ln\left(\sqrt[t]{\prod_{i=1}^{t} f(s^{\text{mut}}, E^{\text{res}}(n))}\right) \\ &= \lim_{t\to\infty} \frac{1}{t}\sum_{i=1}^{t} \ln\left(f(s^{\text{mut}}, E^{\text{res}}(n))\right). \end{aligned} \tag{24}$$

In practice however, it is possible to calculate invasion fitness only in the case of p-periodic resident population dynamics when $p \in \mathbb{N}$. In this case,

$$r(s^{\text{mut}}, E^{\text{res}}) = \frac{1}{p} \sum_{i=1}^{p} \ln \big(f(s^{\text{mut}}, E^{\text{res}}(n)) \big).$$

5.2 Invasion fitness in metapopulations

Defining fitness in metapopulations is not straightforward, since individuals compete with each other in the local patches, but a trait combination that is extremely profilic locally, may be completely destroyed by a catastrophe, if it fails to send out successful dispersers. Below, the calculation of invasion fitness in metapopulations is presented in the case of a monomorphic resident population. The generalization to polymorphic residents is rather straightforward, but notationally more complex.

In metapopulation models, fitness must be determined at the level of dispersers and local clans initiated by the dispersers (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001; Parvinen, 2006). Once a disperser enters a local patch, it starts a new clan. This clan consists of the disperser itself, its descendants, their descendants, etc. Due to clonal reproduction, all the individuals in the clan have the same strategy as the initiating disperser. Depending on this strategy and the local conditions in the patch, the clan may either die out due to the local competition in the patch, or increase in population size until it is destroyed by the next local catastrophe in the patch.

Each generation in the clan sends out new dispersers until the whole clan, as well as the whole local population, is destroyed by a local catastrophe. The expected number of successful dispersers (i.e., initiated new local clans) produced by a local clan can be interpreted as the basic reproduction number of the dispersers (or, equally, of the local clans), and it can be used as a proxy for the invasion fitness as above in well-mixed populations.

In metapopulation models, the environment set by the resident must be determined at the metapopulation level. Throughout this thesis, the ecological parameters are always chosen such that a metapopulation-level quasi-steady state exists (Article 4 that considers non-equilibrium dynamics focuses solely on the well-mixed populations). This means that, at this quasi-equilibrium, the size D of the resident disperser pool is constant. However, as long as local disasters may occur, the local population sizes still vary. After a catastrophe a new local population is immediately founded by the immigrants from the disperser pool. This new local population is, however, usually very small compared to the resident-population's fixed point size set by the resource carrying capacities, the resident strategy and disperser pool size D. The local population size then approaches a stable attractor until the next local disaster occurs. It is even possible that the metapopulation level dynamics have a fixed-point attractor (constant D) even though the local dynamics have cyclic attractors (Gyllenberg et al., 1993). However, in this thesis the main focus is on the metapopulations with local dynamics of the Beverton–Holt type, where population size always approaches a fixed point value monotonically.

In a metapopulation-dynamical equilibrium, the disperser pool size and the distribution of local population sizes remain constant, although the size of the local population in each patch varies. It may be crucial for a mutant, whether it enters a patch that is almost empty after a recent local disaster, or a patch where the local population size has already grown large.

Let now $R(s^{\text{mut}}, E^{\text{res}})$ denote the expected number of new successful dispersers sent out by an average local clan initiated by a strategy s^{mut} disperser in an environment E^{res} set by the strategy s^{res} resident.

Consider a monomorphic resident metapopulation that has settled to a metapopulation-dynamical equilibrium with constant disperser pool size D. Then, all patches of type m and age n (time elapsed since the latest catastrophe in the patch) have the same population density x_n^m. It is easy to iteratively calculate these densities from the equation

$$x_{n+1}^m = (1-e) f^m(s^{\text{res}}, E_{\text{loc}}^{\text{res}}(n)) x_n^m + \pi D, \qquad x_0^m = \pi D, \tag{25}$$

where $E_{\text{loc}}^{\text{res}}(n)$ is the local environment (resource availabilities) in the patch under consideration determined by the local resident population n time-units after the latest local catastrophe. Once the successive resident population densities have been calculated using equation (25), it is possible to further calculate the vector of successive local environmental conditions set by this resident, i.e.,

$$E_{\text{loc}}^{\text{res}} = (E_{\text{loc}}^{\text{res}}(1), E_{\text{loc}}^{\text{res}}(2), \ldots, E_{\text{loc}}^{\text{res}}(n), \ldots).$$

These local resource availabilities allow one to calculate iteratively the dynamics of the mutant clan in this patch as a function of the time elapsed since the latest catastrophe and the time elapsed since the foundation of this clan. The local populations are assumed to be large (mathematically speaking infinite), which allows one, e.g., to neglect demographic stochasticity. Therefore, numbers x_n^m do not represent individuals but some abstract units of population density. It is clearly impossible to determine the size of a mutant clan consisting of only a single mutant individual (or a few mutant individuals) using these units. Fortunately, this is not even necessary, since the mutant population is assumed to be small. Thus, the resident population determines the density-dependent factors in the mutant dynamics, i.e., one can neglect the changes in the resource availabilities caused by the mutants as well as the effects of immigration on the local population dynamics of the mutants. This means that the dynamics of a mutant clan are linear with growth set by the properties of the patch and the resident population densities. Hence, one can use the relative size (actual size divided by the initial size) of the clan to determine how many new successful dispersers a clan is expected to produce.

Let now a local mutant clan with strategy s^{mut} be founded in a type m patch that has encountered its latest local catastrophe η_0 time units ago. Denote the relative size of this clan when η time units have elapsed since the latest catastrophe by $y_{\eta_0}^m(\eta, s^{\text{mut}}, E_{\text{loc}}^{\text{res}})$, where $E_{\text{loc}}^{\text{res}}$ refers to the local environment set by the resident population. Now $\eta - \eta_0$ is the time elapsed since the foundation of this clan.

It is now possible to solve $y_{\eta_0}^m(\eta, s^{\text{mut}}, E_{\text{loc}}^{\text{res}})$ from a linear difference equation

$$\begin{cases} y_{\eta_0}^m(\eta+1, s^{\text{mut}}, E_{\text{loc}}^{\text{res}}) = (1-e) f^m(s^{\text{mut}}, E_{\text{loc}}^{\text{res}}(\eta)) y_{\eta_0}^m(\eta, s^{\text{mut}}, E_{\text{loc}}^{\text{res}}), \\ y_{\eta_0}^m(\eta_0, s^{\text{mut}}, E_{\text{loc}}^{\text{res}}) = 1. \end{cases}$$

Therefore

$$y_{\eta_0}^m(\eta, s^{\text{mut}}, E_{\text{loc}}^{\text{res}}) = \prod_{i=\eta_0}^{\eta-1} (1-e) f^m\big(s^{\text{mut}}, E_{\text{loc}}^{\text{res}}(i)\big). \tag{26}$$

Now, $y^m_{\eta_0}(\eta, s^{\text{mut}}, E^{\text{res}}_{\text{loc}})$ is the size of the mutant clan given that there are no local catastrophes. When calculating the expected number of dispersers produced by this clan, however, the catastrophes have to be taken into account. Furthermore, the exact ordering of the events during season has to be considered also. A local catastrophe destroys the clan along with the entire local population. The clan founded η_0 time units after the latest local catastrophe is still alive $\eta_0 + 1$ time units after the catastrophe with probability $1 - c$, and at the census of that season it has relative size

$$y^m_{\eta_0}(\eta_0 + 1, s^{\text{mut}}, E^{\text{res}}_{\text{loc}}) = (1 - e) f^m(s^{\text{mut}}, E^{\text{res}}_{\text{loc}}(\eta_0)).$$

However, emigration takes place before census, especially before the size of the clan has been diminished by the factor $1 - e$. Therefore, the expected number of successful dispersers produced by the clan in the first season after its foundation is

$$\pi e(1 - c) f^m(s^{\text{mut}}, E^{\text{res}}_{\text{loc}}(\eta_0)) = \pi e(1 - c) \frac{y^m_{\eta_0}(\eta_0 + 1, s^{\text{mut}}, E^{\text{res}}_{\text{loc}})}{1 - e}.$$

This reasoning can be generalized forward, and altogether, the mutant clan is expected to produce

$$\frac{\pi e}{1 - e} \sum_{\eta=\eta_0}^{\infty} (1 - c)^{1+\eta-\eta_0} y^m_{\eta_0}(\eta, s^{\text{mut}}, E^{\text{res}}_{\text{loc}})$$

new successful dispersers.

The probability that the clan is founded in a patch, where η_0 time units have elapsed since the latest local catastrophe, is $(1 - c)^{\eta_0} c$, and the probability that the clan is founded in a type m patch is p_m, the fraction of type m patches. Thus, one can calculate $R(s^{\text{mut}}, E^{\text{res}})$, the expected number of new mutant clans initiated by an average strategy s^{mut} mutant clan in an environment E^{res} set by the resident population, as

$$R(s^{\text{mut}}, E^{\text{res}}) = \sum_m p_m \sum_{\eta_0=0}^{\infty} (1 - c)^{\eta_0} c \left(\frac{e\pi}{1 - e} \sum_{\eta=\eta_0}^{\infty} (1 - c)^{1+\eta-\eta_0} y^m_{\eta_0}(\eta, s^{\text{mut}}, E^{\text{res}}_{\text{loc}}) \right), \tag{27}$$

which simplifies into

$$R(s^{\mathrm{mut}}, E^{\mathrm{res}}) = \frac{e\pi c}{1-e} \sum_{m} p_m \sum_{\eta_0=0}^{\infty} \sum_{\eta=\eta_0}^{\infty} (1-c)^{1+\eta} y_{\eta_0}^{m}(\eta, s^{\mathrm{mut}}, E_{\mathrm{loc}}^{\mathrm{res}}). \quad (28)$$

Until now, it has been assumed that the size D of the resident disperser pool is a known constant. Now, one can finally solve the actual value of D from a fixed point equation

$$R(s^{\mathrm{res}}, E^{\mathrm{res}}) = 1, \quad (29)$$

since in the metapopulation-dynamical quasi-equilibrium, each successful disperser has to produce on average exactly one new successful disperser. In the case of a polymorphic resident population, one obtains one fixed-point equation for each resident strategy, and the sizes of the dispersal pools of each strategy may, in principle, be solved from this equation, but in practice, the actual calculation becomes rapidly overly cumbersome as the amount of resident strategies increases.

Note, that even though the disperser pool size D is not explicitly involved in the equation (29), it affects the values of the environmental interaction variables $E_{\mathrm{loc}}^{\mathrm{res}}$ as it determines the local population density distributions of the residents in each patch. As mentioned before, the interaction variable contains the information about the nonlinear feedback, and thus, the model becomes linear if its value is assumed to be known.

5.3 Environmental interaction variable and the principle of competitive exclusion

The traditional interpretation of the principle of competitive exclusion (Gause, 1934; Hardin, 1960; Levin, 1970; Armstrong and McGehee, 1980) states that at steady state there cannot be more coexisting species (strategies) than there are resources (or other limiting factors). In any model with two distinct resources, including the current model, this would prevent the coexistence of more than two different strategies. However, this statement has already been shown incorrect in several occasions (see, e.g., Wilson and Yoshimura (1994)). The modern version of this principle (Diekmann et al., 2003; Meszéna et al., 2006), however, states that the maximum number of species (strategies) that can robustly coexist at steady state is less than or equal to the dimension of the interaction variable.

In a well-mixed population with a fixed-point attractor, the environmental interaction variable only includes the equilibrium availabilities of the two resources, and hence the maximum number of coexisting strategies is limited to two. However, already in the case of a two-periodic attractor in a well-mixed population, the interaction variable includes two successive availabilities for each resource, and hence its dimension is four. In metapopulation models with quasi-equilibrium dynamics, i.e., fixed disperser pool size even though local population sizes vary due to catastrophes, the dimension of the interaction variable is, in principle, infinite. Thus, the principle of competitive exclusion sets no limits for the coexistence of different strategies, even though the robust coexistence of a continuum of strategies is still not possible (Gyllenberg and Meszéna, 2005).

6 Evolution of resource specialization

6.1 Ways to model specialization

As mentioned at the beginning of this thesis, evolution of specialization affects the dynamics of virtually any other life-history trait. Therefore, it has been studied within numerous frameworks. In this thesis, the focus is on the case of usage of two distinct resources that has been also considered, e.g., by MacArthur and Levins (1964); Lawlor and Maynard Smith (1976); Schreiber and Tobiason (2003); Ma and Levin (2006); Rueffler et al. (2006, 2007) and Abrams (2012). However, evolution of resource utilization has also been widely studied in the case of a single resource with a continuously varying character (see, e.g., MacArthur and Levins (1967); Dieckmann and Doebeli (1999); Kisdi and Geritz (1999); Egas et al. (2005) and, for the case with several resources (Büchi and Vuilleumier, 2014)). This approach relates closely to the studies of niche evolution (see, e.g., Roughgarden (1972, 1976); Abrams (1986); Kassen (2002); Ackermann and Doebeli (2004); Holt (2009)).

Resource continuums have also been studied in the context of ecological character displacement (see, e.g., Brown and Wilson (1956); Slatkin (1980); Grant (1994); Doebeli (1996); Kawecki and Abrams (1999); Mizera and Meszéna (2003)), where the main interest is the co-evolution of two competing species or strategies. In the studies of character displacement, it is usually assumed that there exists, in the environment under consideration, a single optimal phenotype towards which the monomorphic population evolves. However, monomorphic populations or evolutionary branching are not usually considered, but the main focus is on the effects of interspecific competition to the evolution of two competing species, or strategies: How far from the optimal phenotype can the phenotypes of the competing species be driven by the tendency to avoid competition. The ecological character-displacement approach is rather closely related to the theories of optimal foraging (see, e.g., MacArthur and Pianka (1966); Schoener (1971); Charnov (1976); Oaten (1977); Pyke (1984); Stephens and Krebs (1986)).

The evolution of specialization may also be approached from the point of view of phenotypic plasticity (see, e.g., Via and Lande (1985); Moran (1992); Scheiner (1993); van Tienderen (1997); Sultan and Hamish (2002)).

In this case, the specialist strategies correspond to non-plastic phenotypes utilizing one resource, whereas the generalist strategy exhibits phenotypic plasticity being able to utilize both of the resource but less efficiently than the specialists on these resources. The trade-off parameter θ, in this case, measures how limited are the resource consumption abilities of the plastic phenotype compared to the specialist phenotypes (DeWitt et al., 1998).

Biologically more specific models of the evolution of resource specialization have been constructed, e.g., for the analysis of evolution of host specialization of parasites and phytophagous insects, where it is natural to interpret alternative hosts as different resources for the parasite or phytophagous insect (see, e.g., Jaenike (1990); Joshi and Thompson (1995); Fry (1996); Abrams and Kawecki (1999); Nosil (2002); Poulin et al. (2006)). Moreover, in spatially heterogeneous models, different types of suitable habitats may also be considered as resources (habitat specialization, see, e.g., Levins (1962, 1963); van Tienderen (1991); Fryxell (1997); Kisdi (2002); Morris (2003))

Also, diverse modeling approaches have been used. Genetic models (see, e.g., Taper and Chase (1985); Drossel and McKane (1999, 2000); Bürger (2002, 2005); Via (2002)) are able to treat different genetic architectures in detail but usually require one to use rather simple models for the ecological dynamics. Phenotypic models of evolution (Lande, 1976; Emlen, 1980) sometimes lack immediate genetic underpinnings but on the other hand let one to study ecologically more complex systems. The traditional approaches on the phenotypic modeling of evolution of specialization have included for example game theoretic models (see, e.g., Brown (1990); Parker and Maynard Smith (1990); Brown and Vincent (1992); Hofbauer and Sigmund (1998)) and models using the adaptive dynamics approach (see, e.g., Meszéna et al. (1997); Parvinen and Egas (2004); Ma and Levin (2006)).

6.2 Evolution of specialization in well-mixed populations under equilibrium dynamics

Majority of mathematical models focusing on the evolution of specialization assumes a well-mixed population. As a consequence, the possible evolutionary scenarios are, especially in the case of equilibrium population dynamics, rather well-known. In the case of two different resources, the most striking common feature of the evolutionary dynamics is the importance of the trade-off: A strong trade-off between the abilities to utilize the resources leads to specialist populations whereas weak trade-off results in generalist populations. These are the evolutionary scenarios observed when evolution is frequency-independent (Levins (1962, 1963), but see also Rueffler et al. (2004)). However, when selection is frequency-dependent and trade-off is moderately strong, it is possible that evolution of a monomorphic population directs to increased generalism, but the generalist population undergoes evolutionary branching, and finally, the population comprises two different specialist strategies (see, e.g., Meszéna et al. (1997)).

The evolutionary scenarios observed in this thesis correspond to this general overview. They are illustrated in Figure 4. Note that evolutionary branching illustrated in panel B requires that the ecological dynamics are modeled such that the dimension of the environmental interaction variable is at least two (so that selection is frequency-dependent). When there are two resources and the ecological dynamics have an equilibrium attractor, it is rather natural to the environmental interaction variable to have two dimensions (two scalars, each describing the equilibrium availability of one resource). This is the case also in the models analyzed in this thesis. Thus, the modern competitive exclusion principle by Meszéna et al. (2006) prevents the robust coexistence of more that two strategies. However, Rueffler et al. (2006) have shown that there are natural ways to model specialization also such that the interaction variable has only one dimension, which excludes evolutionary branching and robust coexistence of any pair of strategies.

The effect of the trade-off strength (trade-off parameter θ) on the evolutionary dynamics is summarized in Figure 5 that illustrates evolutionary bifurcation diagrams, where the evolutionary singular strategies of a monomorphic population are plotted as a function of θ. It is noteworthy that, the devoted specialist strategies may still maintain their evolutionary attractivity for a while, even though the unbiased generalist strategy becomes evolutionarily attracting as the value of θ increases.

After evolutionary branching, the evolution of the dimorphic population usually directs towards the combination of the two devoted specialist strategies. This is the always case in this thesis when the ecological dynamics have fixed point attractors in a well-mixed population. However,

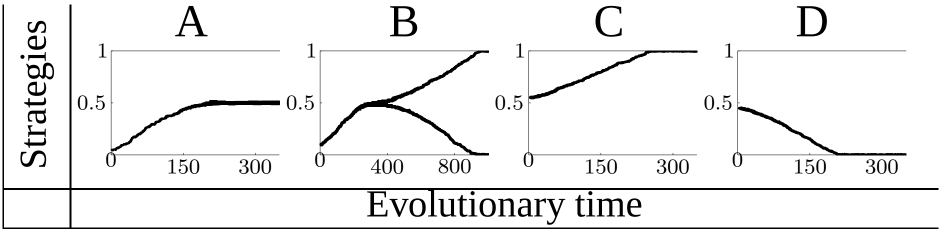

Figure 4: **Evolutionary scenarios under equilibrium population dynamics.**

Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix of Nurmi and Parvinen (2013). Thus, it is only applicable for comparison between different simulations using the same procedure.

Panel A: Concave resource consumption function (weak trade-off) – Evolution leads to generalism.

Panel B: Weakly convex resource consumption function (moderately strong trade-off) – Evolution of a monomorphic population leads to generalism, where evolutionary branching takes place. The evolution of a dimorphic population leads to the combination of the two devoted specialist strategies.

Panels C and D: Strongly convex resource consumption function (strong trade-off)– Evolution leads to the nearest devoted specialist strategy.

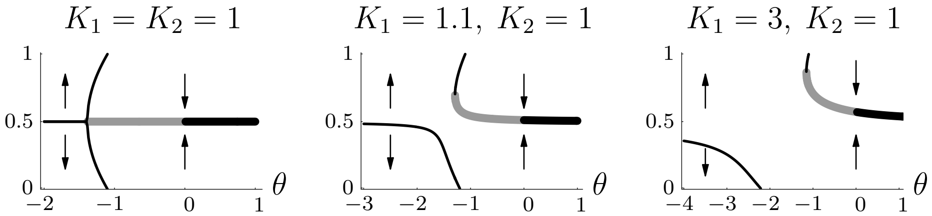

Figure 5: Singular strategies as a function of the trade-off parameter θ when $\lambda = 3$ in the Beverton–Holt model (equation 16). Thin black curve indicates evolutionary repellors, thick grey curve branching points and thick black curve evolutionary endpoints. The arrows in the panels indicate the expected direction of evolution in a monomorphic population. The evolutionary bifurcation diagrams for other corresponding models, e.g., discrete logistic model (equation 18) and Ricker model (equation 19) are qualitatively similar.

Zu et al. (2011a, 2011b) have shown that, for complicated trade-off structures, the evolution of the dimorphic population may lead to a dimorphic singular strategy combination, in which the coexisting strategies are not devoted specialists. Further branching, however, is not possible.

Altogether, there are four different endpoints for the specialization evolution in the models studied in this thesis in well-mixed populations under equilibrium dynamics. None of them, however, involves evolution to the trimorphic coexistence of specialists and generalists. This in in accordance with the majority of previous results, (see, e.g., Brown (1990); Meszéna et al. (1997); Parvinen and Egas (2004); Ma and Levin (2006); Ravigné et al. (2009)). In this thesis, it is explored how this modeling approach could be extended in order to allow evolution starting from a monomorphic population to lead to trimorphic coexistence.

There are several models where the ecological coexistence of a generalist strategy and two specialist strategies is possible (Wilson and Yoshimura, 1994; Kisdi, 2002; Abrams, 2006b). However, such coexistence may often be evolutionarily unstable. Even more rarely is such trimorphic coexistence evolutionarily attainable, i.e., reachable from an initially monomorphic population when mutations are assumed small and infrequent.

The possibility of ecological trimorphic coexistence was first demonstrated in a model compiled by Wilson and Yoshimura (1994). However, Egas et al. (2004) showed that this coexistence is not evolutionary attainable, and furthermore, evolution even destroys the coexistence. Later on, trimorphic coexistence has been shown evolutionarily attainable under cyclic resource dynamics (Abrams, 2006a,b), or when the assumptions concerning the consumer behavior are relatively restrictive (Egas et al., 2004), or only in a narrow parameter domain (Kisdi, 2002). In spatially heterogeneous model with spatially aggregated resources, distance-limited dispersal may also allow evolutionarily attainable trimorphic coexistence such that generalists live in the habitat boundaries (Débarre and Lenormand, 2011; Karonen, 2011).

Below, different extensions of the well-mixed consumer population model with two resources are introduced, that allow the evolution to the trimorphic coexistence of specialists and generalists.

6.3 Evolution of specialization in the case of well-mixed populations with non-equilibrium dynamics

In the context of dispersal evolution, the importance of non-equilibrium ecological dynamics has been recognized for a long time. On one hand, non-equilibrium population dynamics may forge dispersal and even enable evolutionary branching of dispersal strategies, but, on the other hand, dispersal may stabilize population dynamics (Gyllenberg et al., 1993; Holt and McPeek, 1996; Parvinen, 1999; Ronce, 2007). However, recent results indicate that the type of population-dynamical attractor may affect the evolution of other life history traits as well (White et al., 2006; Geritz et al., 2007; Hoyle et al., 2011). Previous work on other traits has shown that, under non-equilibrium population dynamics, evolutionary branching may be possible also in such ecological scenarios that do not allow branching under equilibrium dynamics (Parvinen, 1999; White et al., 2006; Hoyle et al., 2011). Thus, non-equilibrium dynamics may result in enhanced biodiversity.

In the model analyzed in this thesis, evolutionary branching is possible already under equilibrium dynamics. However, non-equilibrium dynamics may still add in diversity by allowing a secondary evolutionary branching to occur, which results in the trimorphic coexistence of generalists and specialists. Furthermore, non-equilibrium dynamics may result in evolutionary suicide. Below, these evolutionary scenarios enabled by the non-equilibrium dynamics are presented by illustrating results of evolutionary simulations.

In order to illuminate how the population dynamics affect the evolutionary dynamics, one needs to illustrate the population-dynamical attractors during the evolutionary time together with the evolutionary tree in the strategy space. However, the evolutionary simulations are never completely mutation limited. Instead, the population is, in practice, always polymorphic during the simulation. Therefore, in order to illustrate the population-dynamical attractor of the entire population, one needs to calculate how much extant strategies use resources, which in turn allows one to calculate the availabilities of the resources. If strategies $(s^{(1)}, s^{(2)}, \ldots, s^{(k)})$ are present at time unit n with corresponding population sizes $(x_n^{(1)}, x_n^{(2)}, \ldots, x_n^{(k)})$, then the availabilities of the resources 1 and 2 are for the case with logistic ecological dynamics, according to equations 9 and 17, respectively

$$\begin{aligned} \widehat{A}_n^{(1)} &= K_1 \max\left(0, 1 - \textstyle\sum_{i=1}^{k} \beta(s^{(i)}) x_n^{(i)}\right) \\ \widehat{A}_n^{(2)} &= K_2 \max\left(0, 1 - \textstyle\sum_{i=1}^{k} \beta(1 - s^{(i)}) x_n^{(i)}\right). \end{aligned} \tag{30}$$

When the population is on a non-equilibrium attractor, these availabilities fluctuate as the consumer population sizes fluctuate. Based on these availabilities, it is often possible to deduce the type of the population-dynamical attractor of the consumer population as a whole. For example in the case with two equally abundant resources, if the population is on a two-periodic in-phase orbit, the sum of the resource availabilities takes two different values on the population-dynamical attractor whereas their difference is close to zero. If the population is on a two-periodic out-of-phase orbit (asymmetric attractor), the differences alternate between a positive and a negative value on the population-dynamical attractor whereas the sum remains virtually constant. More generally: the more asynchronous are the resource fluctuations, the larger are the absolute values of the differences in the resource availabilities.

Evolution to singular dimorphic strategy pairs

Under non-equilibrium dynamics, dimorphic evolution may lead to singular strategy pairs instead of pairs of devoted specialist strategies even when the trade-off function is everywhere convex (concave). On one hand, Nurmi and Parvinen (2013) showed that, under in-phase oscillations of the resource availabilities, a dimorphic population usually evolves towards the combination of the two devoted specialist strategies when parameter values are such that a monomorhic population evolves to generalism where evolutionary branching takes place. On the other hand, asynchronous oscillations of the resource availabilities may benefit generalists, since the generalists experience less variance in the resource intake.

Evolutionary dynamics, in this case increasing specialism, may cause attractor switches to the ecological dynamics. Due to the effects introduced above, these attractor switches may stop the dimorphic evolution to a singular dimorphic strategy pair as illustrated in the Figure 6. Furthermore, under chaotic population dynamics, it is even possible that the stochastic mutations, even though they are small in effect, induce attractor-switches in the ecological dynamics. These attractor switches may sometimes generate evolutionary fluctuations (illustrated in Nurmi and Parvinen (2013)).

Evolution to the trimorphic coexistence of a generalist with two specialist

Evolution starting from a monomorphic population may, under non-equilibrium population dynamics, lead to the trimorphic coexistence of a generalist and two specialists strategies. In such coexistence, each of the specialists uses the corresponding resource more efficiently than the competing strategies. The viability of the generalist strategy, on the other hand, is based on the asynchronous non-equilibrium population dynamics of the specialists. The population sizes of the specialist strategies fluctuate, and hence they are repeatedly rather low, which means that the corresponding resource is abundantly available allowing the generalist to increase in population size. This phenomenon was originally observed by Abrams (2006b,a) in a continuous-time model involving Holling type II functional response in the case where the dynamics of the two resources are different, which creates sufficient asynchrony to the resource dynamics. However, non-linear functional response is known to have an essential part in allowing species coexistence, e.g., several species can coexist even on a

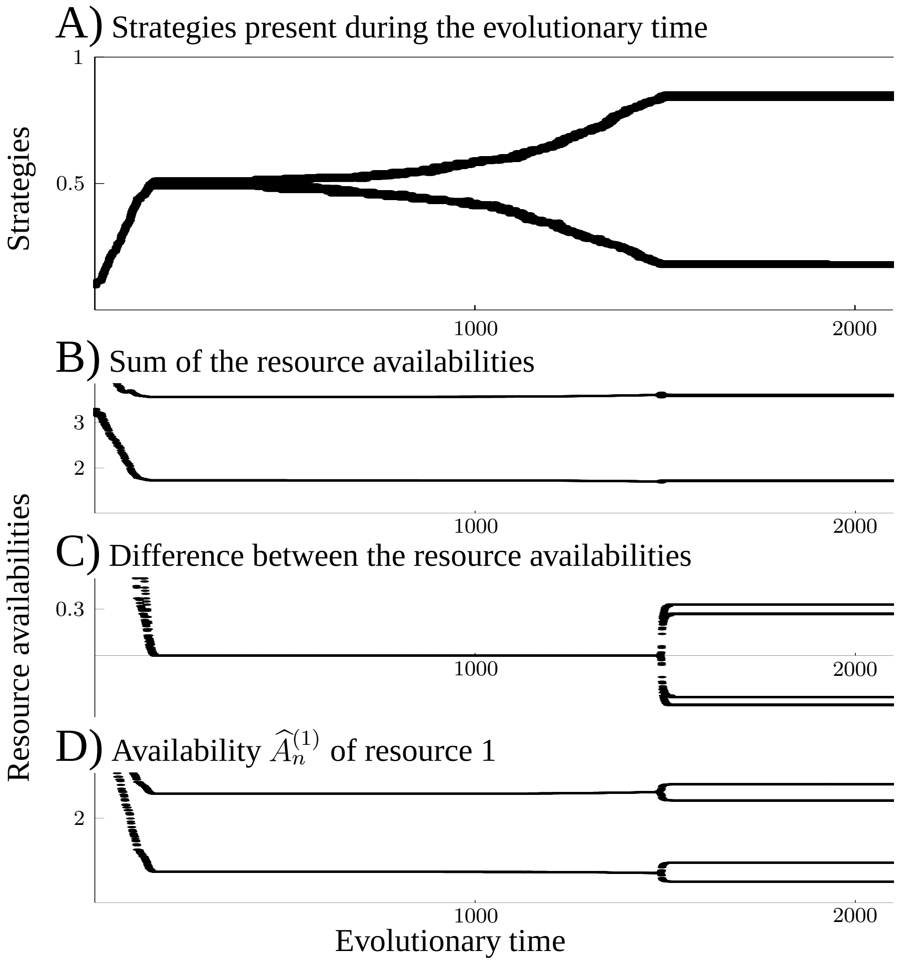

Figure 6: **The result of an evolutionary simulation leading to a dimorphic singular strategy pair under periodic population dynamics in the logistic model (equation 18).**

Panel A: Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix of Nurmi and Parvinen (2013). Thus, it is only applicable for comparison between different simulations using the same procedure.

Panels B, C, and D: Resource availabilities $\widehat{A}_n^{(1)}$ and $\widehat{A}_n^{(2)}$ as defined in equation (30) as a function of the evolutionary time. For each evolutionary time unit, Panel B illustrates the sum of the resources availabilities during each step on the population-dynamical attractor. Panel C illustrates the differences of the resource availabilities and panel D the availability of resource 1.

Parameters: $K_1 = K_2 = 3.5,\ \theta = -0.1,\ \alpha_1 = \alpha_2 = 1,\ \lambda_1 = \lambda_2 = 1.$

single resource under non-equilibrium dynamics (Armstrong and McGehee, 1980; Kisdi and Liu, 2006; Geritz et al., 2007; Tachikawa, 2008).

In the models analyzed in this thesis, consumers use resources according to the law of mass-action with a linear functional response (Holling type I functional response). Furthermore, evolution to trimorphic coexistence is possible also in the case of similar resources since the asynchronous fluctuations in the resource availabilities may be generated solely by the over-compensatory consumer population dynamics. Thus, the results indicate that non-equilibrium population dynamics really is the main factor enabling evolution to trimorphic coexistence.

Figure 7 illustrates an example of an evolutionary simulation leading to trimorphic coexistence. There, the population first evolves to generalism, where evolutionary branching occurs. After branching, the dimorphic population ”inherits” its population-dynamical attractor from the preceding monomorphic population Geritz et al. (2002). Thus, the dimorphic population is initially on an in-phase two-periodic orbit. Therefore, the dimorphic population evolves initially towards the coexistence of the two devoted specialists. However, as the branches specialize further, their ecological dynamics undergoes a series of period-doubling bifurcation which leads to chaotic ecological dynamics, which breaks the synchronism in the dynamics of the two morphs. Finally, the population-dynamical attractor becomes an out-of-phase two-periodic orbit, where the evolutionary dynamics lead to a singular dimorphic strategy pair, which is not uninvadable, and thus, a secondary evolutionary branching occurs and leads to trimorphic coexistence.

Evolutionary suicide and branching–extinction cycles

The possibility of evolutionary suicide relates to one peculiarity of the discrete-time version of the logistic population model: if the resources are abundant and the consumers use them efficiently, it is possible that one or both of the resources become exhausted. It is not possible to produce new eggs by utilizing an exhausted resource. Thus, if both resources are exhausted simultaneously, all the consumers die out even though the resources recover later. If one of the resources becomes exhausted, all the devoted specialists utilizing this resource die out. Both of these scenarios may lead to evolutionary suicide and the latter one even to evolutionary

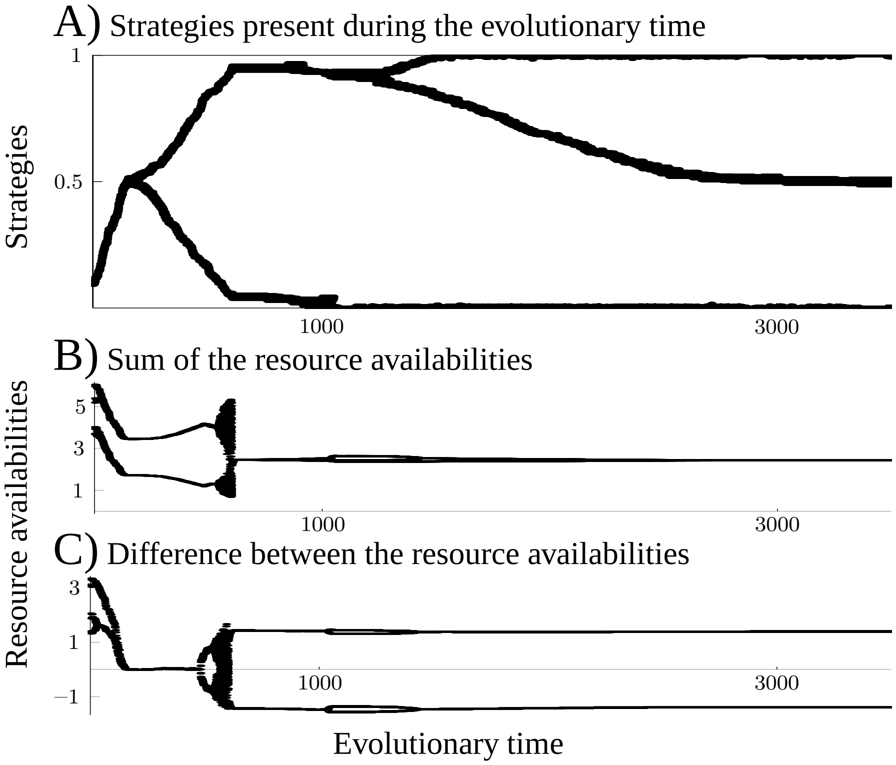

Figure 7: **The result of an evolutionary simulation leading to the co-existence of generalist and specialists in the logistic model (equation 18).**

Panel A: Strategies present in the population as a function of the evolutionary time. One unit of evolutionary time corresponds to one loop of the simulation procedure depicted in the Appendix of Nurmi and Parvinen (2013). Thus, it is only applicable for comparison between different simulations using the same procedure. Initial population is monomorphic practicing strategy $s = 0.1$. Simulation ended in a trimorphic population practicing strategies $s_1 = 0$, $s_2 = 0.5$, and $s_3 = 1$.

Panels B and C: Resource availabilities $\widehat{A}_n^{(1)}$ and $\widehat{A}_n^{(2)}$ as defined in equation (30) as a function of the evolutionary time. For each evolutionary time unit, Panel B illustrates the sum of the resources availabilities during each step on the population-dynamical attractor. Panel C illustrates the differences of the resource availabilities.

Parameters: $K_1 = K_2 = 3.8,\ \theta = -0.72,\ \alpha_1 = \alpha_2 = 1,\ \lambda_1 = \lambda_2 = 1.$

branching–extinction cycles (see Nurmi and Parvinen (2013) for illustrations). However, in the latter scenario, the possibility of evolutionary suicide in evolutionary simulations depends on the details of the simulation procedure (see the Appendix of Nurmi and Parvinen (2013)).

An overview of the evolutionary dynamics under non-equilibrium population dynamics

A concise overview of the evolutionary dynamics under non-equilibrium dynamics is presented by the way of evolutionary bifurcation diagram in Figure 8. Since the current adaptive dynamics toolbox suffices only for algebraic analyses of the cases with equilibrium or periodic population dynamics, the evolutionary bifurcation diagram has to be complemented by illustrating the endpoints of evolutionary simulations that are based on procedure presented in the Appendix of (Nurmi and Parvinen, 2013).

In Figure 8, if the trade-off is sufficiently strong ($\theta \lesssim -2.4$), the population always evolves to a monomorphic specialist population with chaotic population dynamics. If $-2.4 \lesssim \theta \lesssim -1.7$, the initial strategy of the population determines, whether the population evolves to a monomorphic specialist population, or, via evolutionary branching, to a dimorphic population comprising two devoted specialist strategies. If $-1.7 \lesssim \theta \lesssim -0.87$, evolutionary branching occurs independent of the initial strategy, and evolution leads to a dimorphic combination of the devoted specialist strategies. When $-0.86 \lesssim \theta \lesssim -0.585$, one observes evolution to trimorphic coexistence. In the parameter domain $-0.585 \lesssim \theta \lesssim 0,$ evolution leads to dimorphic singular strategy pairs and evolutionary fluctuations caused by attractor switches of the chaotic ecological dynamics.

When $0 \lesssim \theta \lesssim 0.35$, evolution of specialization ends in a monomorphic unbiased generalist population. If $0.35 \lesssim \theta$, evolution still directs towards generalism, but increasing benefit obtained from generalism together with high resource carrying capacities finally results in overly extensive resource usage exhausting both resource simultaneously, which results in evolutionary suicide, and thus, evolutionary simulations end to extinction at the boundary of the black area indicating unviable strategies in the evolutionary bifurcation diagram.

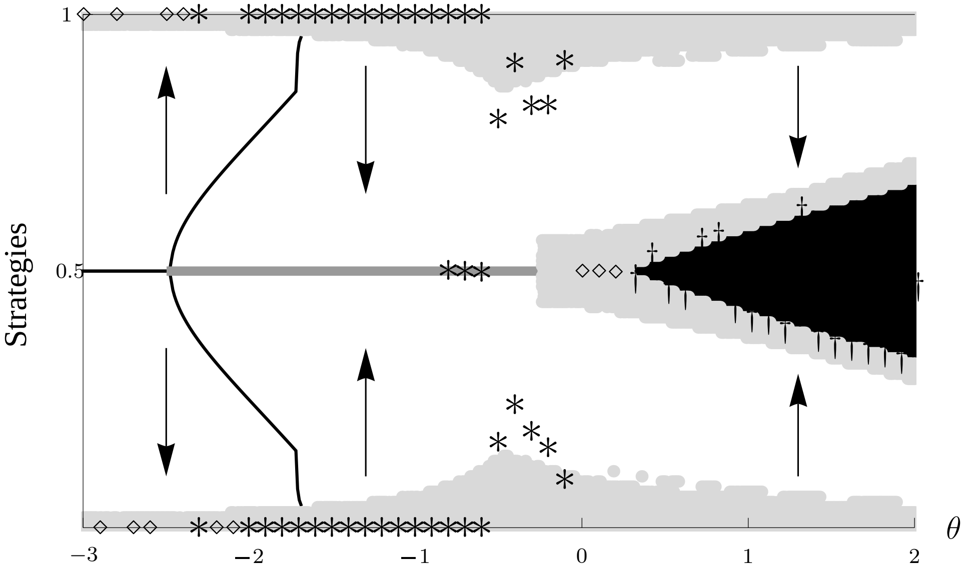

Figure 8: **Evolutionary bifurcation diagrams in the case of possibly non-equilibrium population dynamics in the logistic model (equation 18).** Singular strategies and endpoints of evolutionary simulations as a function of the trade-off parameter θ when specialists have chaotic population dynamics. Biased usage of two resources may stabilize population dynamics, but high benefit of generalism enables chaotic dynamics and even evolutionary suicide.

Thin black curve indicates evolutionary repellors and thick grey curve branching points. The arrows indicate the expected direction of evolution in a monomorphic population. In the black-colored parameter domain, the population is not viable. In the grey-colored parameter domain, the monomorphic population dynamics are (nearly) chaotic.

The evolutionary simulations are initiated in a monomorphic population with random strategy. If an evolutionary simulation ends in a monomorphic population, the end-strategy is denoted by $\diamond$. If it ends in a dimorphic or polymorphic population, the strategies comprising the endpoint are denoted by $*$-signs. If evolutionary suicide occurs, the last viable strategy is denoted by †-sign.

Other parameter values: $K_1 = K_2 = 3.8,\ \alpha_1 = \alpha_2 = 1,\ \lambda_1 = \lambda_2 = 1.$

Altogether, Figure 8 illustrates the qualitative overview of the evolutionary dynamics in the discrete-time logistic population model with non-equilibrium dynamics. The cases with local dynamics determined by the Ricker (1954) or Hassell (1975) models are qualitatively almost similar. In all of these models, there exists a parameter domain where, in the dimorphic population, a secondary evolutionary branching occurs, and the population starts to evolve towards trimorphic coexistence. According to the observations of Nurmi and Parvinen (2013), in the logistic model the evolution in this case always ends to trimorphic coexistence. Evolution to trimorphic coexistence is possible in Ricker and Hassell models as well, but in addition, there exists also a parameter domain, where the appearance of the generalist strategy affects the ecological conditions: As the generalist strategy becomes more unbiased and more common, it synchronizes the resource dynamics such that the generalist itself becomes unviable and goes extinct. Thus, the population becomes dimorphic again making way to a new evolutionary branching and evolutionary cycles (Nurmi and Parvinen, 2013).

6.4 Spatially heterogeneous models for the evolution of specialization and the joint evolution of dispersal propensity and specialization

Spatial heterogeneity usually makes mathematical models more difficult to analyze. A temptingly simple approach to include spatial aspects into the models is to resort to individual-based models where the current location defines the resource availabilities of an individual (Kawata, 1996; Doebeli and Dieckmann, 2000, 2004). However, even though the increasing computational power of modern computers allows ever larger and more detailed models to be analyzed, it is always easier to extract patterns from these models when they can be backed up by theoretical models.

Another simple way to add spatial heterogeneity is to study systems where two (or several) patches are connected by dispersal (van Tienderen, 1991; Wilson and Yoshimura, 1994; Abrams, 1999; Kisdi and Geritz, 1999; Abrams, 2000a; Day, 2000). This approach is, naturally, not able to include the possibility of local catastrophes, even though Kisdi (2002) included the possibility of ”good” and ”bad” years independently in each patch.

Majority of theoretical studies considering evolution of specialization in spatially heterogeneous environments has taken place within the context of evolution of habitat specialization (Levins, 1962, 1963; van Tienderen, 1991; Brown and Pavlovic, 1992; Kisdi, 2002), where it is generally assumed that there is a trade-off between individual’s performances in two different environments or habitat patch types. The results published by Gyllenberg & Metz (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) provided tools that allowed Parvinen and Egas (2004) to consider habitat specialization even within the framework of structured metapopulation models with local catastrophes and infinitely many patches (but only two different patch types).

The habitat specialization approach has two obvious weaknesses. First of all, it usually limits to the cases with only two different patch types and, secondly, it does not determine the origins of the differences between the patch types, and thus, prevents the mechanistic derivation of the local population dynamics. In this thesis, the derivation of the metapopulation theory for the evolution of specialization, initiated by Parvinen and Egas (2004), is continued.

Nurmi et al. (2008) rationalize the differences between the patch types on the basis of different resource availabilities and focus on the evolution of resource utilization. The modeling approach used by Nurmi et al. (2008) resembles the habitat specialization or habitat usage models, but enables the inclusion of several patch types, which, intuitively, might facilitate the coexistence of specialists and generalists.

However, price paid for the conformity with habitat usage models in the model of Nurmi et al. (2008) is that the local resource dynamics within the habitat patches are omitted, and the resource availabilities simply determine, for each patch, a”quality” that delineates the local population dynamics, but unfortunately does not enable mechanistic derivation of the local population dynamics starting from the individual level. Thus, even though the model by Nurmi et al. (2008) was a step forward from the habitat usage models, there was still, in terms presented by Rueffler et al. (2006), an obvious need for the evolutionary analysis of the models that take into account the local resource–consumer dynamics. This deficiency was fixed by Nurmi and Parvinen (2008), who analyzed the model introduced in section 4.

Both Nurmi et al. (2008) and Nurmi and Parvinen (2008) considered evolutionary effects of various ecological parameters and sought for possibilities for trimorphic coexistence. When studying the evolutionary effects of ecological parameters, it was found that the relation between dispersal propensity and the evolution of specialization is rather complicated and can even be counterintuitive. This prompted Nurmi and Parvinen (2011) to study the joint evolution of specialization and dispersal propensity. This study revealed several mechanisms that enable evolution to trimorphic coexistence, and moreover, Nurmi and Parvinen (2011) enabled the analysis of the evolutionary effects of various ecological parameters in a setting where the dispersal propensity is, instead of a preassumed value, assumed to have evolved to the corresponding evolutionarily singular (attracting and uninvadable) value. Nurmi and Parvinen (2008) showed also that evolution of specialization may, in metapopulations, end to a dimorhic singular strategy pair. This may, as presented by Nurmi and Parvinen (2011), be an important step on the path to trimorphic coexistence.

When analyzing the joint evolution of dispersal propensity and specialization, one needs to understand also the evolution of dispersal propensity. Therefore, at this point, a small interlude introducing the main aspects of dispersal evolution is necessary.

Evolution of dispersal propensity

Its rather typical that the evolutionary dynamics of dispersal have only a single evolutionarily singular dispersal propensity, which is always evolutionarily attracting (see, e.g., Johnson and Gaines (1990); Levin et al. (2003) and Ronce (2007)). This is the case also in the models studied in this thesis. The numerical value of this propensity is primarily determined by the catastrophe probability c and the probability π of surviving dispersal. The higher is the probability π, the higher is the singular dispersal propensity. When there remains any risk of dispersal ($\pi < 1$), the catastrophe probability affects the singular dispersal propensity in a non-monotonous way: in the absence of catastrophes ($c = 0$), all local populations stay at the fixed point of the local dynamics, and thus, the strategy not to disperse is an evolutionarily attracting singular strategy, as proved by Parvinen (2006) for the class of structured discrete-time metapopulation models studied in this thesis. As the catastrophe probability increases, the singular dispersal propensity increases in the beginning, too. This is due to the fact that catastrophes result in empty patches, which make dispersal profitable. As the catastrophe probability increases further, most individuals find themselves in sparsely populated patches with plenty of resources. This decreases the advantages of dispersal and causes the singular dispersal propensity to diminish. The value of the singular dispersal propensity reaches zero again at the threshold where the metapopulation loses its viability. This phenomenon has been observed also by, e.g., Ronce et al. (2000); Gyllenberg et al. (2002); Parvinen et al. (2003) and Parvinen (2006). In this thesis, the focus is mainly on the parameter domain in which the singular dispersal propensity appears as an increasing function of the catastrophe probability.

Various mechanisms resulting in evolutionary branching or polymorphisms of dispersal have been observed in different metapopulation models. These mechanisms include temporal variation in form of cyclic (Doebeli and Ruxton, 1997; Parvinen, 1999) or chaotic (Holt and McPeek, 1996) local population dynamics, or temporally and spatially varying carrying capacities (McPeek and Holt, 1992; Mathias et al., 2001). However, catastrophes alone, have been observed not to create enough temporal variation to promote branching. For example, Gyllenberg et al. (2002) did not find evolutionary branching in a structured metapopulation model defined in continuous time with one patch type. Parvinen (2002) studied the corresponding model with several patch types, and observed that catastrophes together with spatial heterogeneity in the sense of different patch types can result in evolutionary branching of dispersal. The necessary level of spatial heterogeneity can be obtained with differences in growth conditions alone, as well as with differences in catastrophe rates alone. A similar observation in a metapopulation model with small local populations, and therefore, locally stochastic population dynamics, was made by Parvinen et al. (2003) (one patch type) and Parvinen and Metz (2008) (several patch types).

Parvinen (2006) studied a discrete-time metapopulation model and found another additional mechanism, which can together with catastrophes result in evolutionary branching. Even though all local populations would eventually reach an equilibrium population size, if they are not hit by a catastrophe, this convergence to the equilibrium can be non-monotonous due to overcompensation in the local discrete-time dynamics, such as in the Ricker model. Parvinen (2006) observed that such temporal heterogeneity together with catastrophes can result in evolutionary branching of dispersal.

In this thesis, the joint evolution of dispersal propensity and specialization is explored only in the case where local population dynamics of the metapopulation are of the Beverton-Holt type, where convergence to the population-dynamical equilibrium is monotonous. Therefore the mechanism for evolutionary branching of dispersal observed by Parvinen (2006) is not present here. Thus, the effects of non-equilibrium dynamics to this joint evolution remains an interesting question for the future research.

In the case of Beverton–Holt-type local dynamics, the evolutionarily singular dispersal propensity is in most cases uninvadable by mutants featuring a different dispersal propensity. In accordance with the reasoning above, Nurmi and Parvinen (2011) observed evolutionary branching of dispersal, if individuals encounter a sufficient amount of spatial heterogeneity in the sense of different patch types (Parvinen, 2002).

The living conditions of generalists in a specific patch are determined by the overall availability of the two resources, whereas the living conditions of specialist are determined solely by the availability of a single resource. With spatially and temporally varying resource availabilities, the former naturally presents less spatial variance that the latter. Therefore, the evolutionary branching of dispersal propensity may be impossible in a generalist population even though it is possible in a specialist population under otherwise similar ecological conditions. Especially, an unbiased generalist regards the two resources as identical and therefore it observes no difference between two patches with swapped resource carrying capacities ($K_1^1 = K_2^2$ and $K_2^1 = K_1^2$). Thus, Nurmi and Parvinen (2011) conjectured that evolutionary branching of dispersal is not possible in a metapopulation comprising unbiased generalist individuals in an environment comprising two patch types with swapped carrying capacities. For a specialist, evolutionary branching of dispersal propensity in such an environment is possible.

Evolution of dispersal is, in a sense, an inviting field of research, since externally determined trade-offs are not necessary but the evolution of dispersal always takes place in the balance between the costs and benefits of dispersal (risks and costs of dispersal versus the benefits gained from, e.g., the colonization of new areas (Hamilton and May, 1977)). Hence, there has been a wide range of research focusing in the evolution of dispersal. However, when both dispersal and ecological specialization may evolve, the mathematical models become notably more complex. Thus, there have been only a few studies exploring this area (Kisdi, 2002; Hanski and Heino, 2003; Heinz et al., 2009; Scheiner et al., 2012).

(Scheiner et al., 2012) analyze the joint evolution of phenotypic plasticity and dispersal using individual-based simulations. They do not observe evolutionary branching of dispersal, which is the key ingredient of all the non-trivial results of Nurmi and Parvinen (2013). Instead in their results, high dispersal is always accompanied with phenotypic plasticity whereas low dispersal leads to genetic differentiation, especially in the presence of cost of plasticity. Hanski and Heino (2003) have carried out a simulation-based case study on the evolution of dispersal and host-plant preference (specialization) among Glanville fritillary butterflies (*Melitaea cinxia*). Their model is parametrized on the basis of observing the actual metapopulation in the Åland Islands in south-western Finland. This field-biologically inclined approach differs notably from the approach of this thesis, where the aim is to explore the biologically realistic parameter domain in order to find different possible evolutionary scenarios. Heinz et al. (2009) have studied the joint evolution of dispersal distance and local adaptation in an environment with a continuously varying character by means of individual-based simulation models both with clonal and sexual reproduction. Their viewpoint is different from the viewpoint of this thesis, but noteworthily in their model, predictions based on asexual model are, qualitatively speaking, principally consistent with the predictions derived from the sexual model. Kisdi (2002) explores a two-patch model in which the evolving traits are dispersal propensity and the adaption to the local conditions in different patches. Compared to the metapopulation models with local catastrophes, she assumes rather mild temporal variations: ”good” and ”bad” years that occur randomly and independently in each patch. These temporal variations are not influential enough to allow selection for high dispersal. Thus, a high degree of dispersal or generalism usually appeared only as a response to the competition with low-dispersal specialists. Kisdi (2002) also observes evolution to the trimorphic coexistence of the specialists and generalists, but only on an extremely narrow parameter domain.

Evolution to a singular dimorphic strategy pair

In a well-mixed population with globally convex (concave) trade-off functions (given by, e.g., equation 20), the usage of two resources evolves to generalism with concave trade-off curves ($\theta > 0$), and to devoted specialism with convex trade-off curves ($\theta < 0$). Under frequency-dependent selection, it is also possible that evolutionary branching occurs and the population evolves to the combination of the two devoted specialists. However, evolution to any other singular dimorphic strategy combination requires rather complex trade-off structures (Zu et al., 2011a, 2011b).

Figure 9A illustrates two evolutionary scenarios brought in by the metapopulation structure (when only the specialization strategy evolves). On one hand, a metapopulation structure may enable evolutionary branching also when it is not possible in well-mixed populations ($\theta > 0$, i.e., weak trade-off). Note that, sometimes, spatial structure may also inhibit diversification (Day, 2000, 2001). On the other hand, Figure 9A illustrates that, within a metapopulation structure, the evolution of specialization may, even for simple trade-off curves, end in a singular dimorphic strategy combination, where the involved strategies are not devoted specialists.

Evolution to trimorphic coexistence

In structured metapopulation models of the type characterized by the equations 21 and 22, the competitive exclusion principle (Meszéna et al., 2006), i.e., the dimension of the environmental interaction variable never limits the number of coexisting strategies. In fact, the possibility for ecological coexistence of a generalist strategy with two specialist strategies is rather firmly built into the metapopulation models where patch types are determined by the carrying capacities (or availabilities) of two resources.

Trimorphic coexistence may occur, for example, in landscapes that consist of equal amounts of three different patch types such that in one patch type resource 1 is abundant and resource 2 scarce, in one patch type resource 2 is abundant and resource 1 scarce and in one patch type both of the resources are equally abundant. If furthermore, the generalist has even

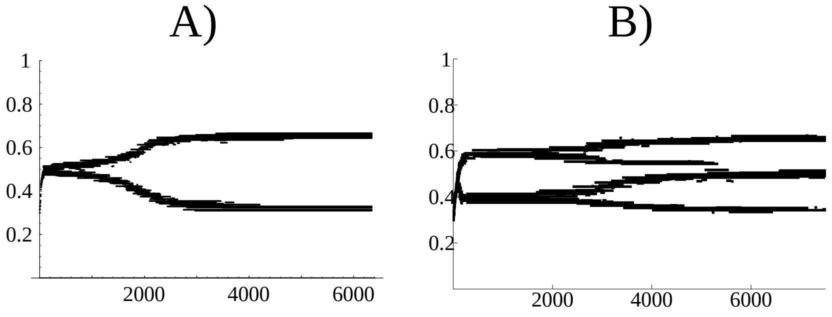

Figure 9: Result of evolutionary simulations where only specialization evolves in a metapopulation model with local dynamics of the Beverton–Holt type (equation 16).
Panel A: Evolution ends to a singular dimorphic strategy combination in an environment comprising two patch types with moderate catastrophe probability. Parameter values: $\theta = 0.1, c = 0.05,\ \lambda = 3,\ e = 0.3,\ \pi = 0.8,\ K_1^1 = K_2^2 = 3,\ K_1^2 = K_2^1 = 1$ and $p_1 = p_2 = 0.5$.
Panel B: Evolution ends to the trimorphic coexistence of two partially specialized strategies and the unbiased generalist strategy in an environment comprising three patch types when catastrophes are extremely rare. Parameter values: $\theta = 0.1, c = 0.0001,\ \lambda = 3,\ e = 0.3,\ \pi = 0.9,\ K_1^1 = K_2^2 = 3,\ K_1^3 = K_2^3 = 2, p_1 = p_2 = 0.25$ and $p_3 = 0.5$.

a small advantage ($\theta > 0$), then the generalist is a superior competitor in patches with equal amount of the two resources, whereas the specialists are superior competitors in patches rich in resource they are specialized to. Now, all the three morphs have patches that they can take over in the long run (if the patch avoids local catastrophes sufficiently long).

Assume now, that catastrophes are extremely rare. Then it is possible to assume an extremely low dispersal propensity without losing the viability of the metapopulation. Then the local dynamics within the patches are virtually independent of each other, with dispersal only allowing slow recolonization of the patches emptied by the local catastrophes. Moreover, due to extremely small catastrophe probability, the patches are virtually always fully occupied, which means, that the type that is best adapted to a certain patch, will outcompete all the other types from this patch, and the immigrants adapted to other patch types will be rapidly ousted, which makes the ecological dynamics in different patches virtually independent.

This mechanism allows the evolution to trimorphic coexistence as illustrated in figure 9B. A similar mechanism may also affect the rich variety of the patterns of local adaptation observed in some species (or clades) inhabiting extremely isolated but stable habitats, such as the Galápagos finches (Darwin, 1845; Grant and Grant, 2002).

Altogether, in the models studied in this thesis, the evolution of specialization hardly ever leads to trimorphic coexistence under equilibrium population dynamics with moderate catastrophe probabilities when only specialization can evolve. This is largely related to the dispersal process: dispersal is assumed to be completely global and random. Distance-limited dispersal together with spatially aggregated resource availabilities is known to enable trimorphic coexistence (Débarre and Lenormand, 2011; Karonen, 2011). Moreover, the evolutionary dynamics of specialization, and thus, the possibilities of trimorphic coexistence, are affected by form of habitat selection, i.e., whether a dispersing individual is able to assess different habitats and choose its target patch according to its characteristics (Rosenzweig, 1981, 1987, 1991; Richards and De Roos, 2001; Ravigné et al., 2004, 2009).

In this thesis, evolution to trimorphic coexistence is more likely under equilibrium population dynamics when both dispersal propensity and specialization may evolve. A typical evolutionary scenario resulting in such coexistence is illustrated in Figure 10. In this figure, local dynamics are of the Beverton–Holt type and the environment is symmetric, i.e., the two resources are, on average, equally abundant. However, since there are three patch types, it is possible to find such parameter combinations that the branching of the dispersal propensity is possible in a metapopulation comprising generalists, and that the dispersal propensity significantly affects the invadability of the generalist strategy.

After the initial phase of evolutionary branching of dispersal propensity, the two branches diverge further apart from each other and, given that trade-off parameter θ has an appropriate value, the generalist strategy may turn from an ESS to an evolutionary branching point for the less dispersive morph. This results in evolutionary branching of the specialization strategy employed by the scarcely dispersing morph, and finally in trimorphic coexistence, in which each of the three morphs has patches where it is a superior competitor and can outcompete the other morphs given that the patch avoids local catastrophes sufficiently long.

Note that although panel A in Figure 10 may seem to indicate a degenerate case in which specialization divides in three branches, this is not the case. Instead, after evolutionary branching of dispersal, both morphs employ the same specialization strategy, $s = 0.5$. The morph with low dispersal propensity undergoes branching of specialization into two branches, while the specialization strategy of the high-dispersal morph remains at $s = 0.5$ as illustrated in Figures 10B-F.

Each evolutionary path leading to trimorphic coexistence observed by Nurmi and Parvinen (2011) involves an evolutionary branching of dispersal propensity in a nearly generalist metapopulation and such parameter combinations that dispersal propensity affects the invadability of the (unbiased or biased) generalist strategies. In environments comprising only two different patch types, it is rather difficult to find such ecological settings, and evolution rarely leads to the coexistence of specialists and generalists. However, this possible at least in two ways (in narrow parameter domains).

Figure 11 illustrates the scenario, where evolution to trimorphic coexistence is possible even in a symmetric environment (resources are on averages equally abundant) comprising only two patch types. There, in a monomorphic population, evolution leads to a singular dimorphic strategy combination. Even though evolutionary branching of the dispersal propensity is not possible in a metapopulation comprising unbiased generalists (since they observe only one patch type), it is possible for both of these partially specialized strategies. As the environment is symmetric, and thus, the evolutionary forces acting on both branches are symmetric, also the events of evolutionary branching occur fairly simultaneously (for most sequences of stochastic mutation events).

Thus for a while, the population becomes quadrimorphic, and the more dispersive morphs start to evolve towards generalism while the less dispersive morphs become more specialized. Finally, either both of the more dispersive morphs converge to generalism or one of them dies out and the other converges to generalism. In the resulting trimorphism the more dispersive morph finds its niche by efficiently colonizing patches emptied by catastrophes. On the other hand, the low dispersal specialists get along as, in the long run, they can take over the patches rich in the resource they are specialized in. Recently, Nagelkerke and Menken (2013) showed, in a Levins-type metapopulation model, that this kind of ecological coexistence may possible even without differences in the dispersal propensities if the specialists can live only on a single patch type while generalists can inhabit any patch type, since in this case the generalists can colonize new patches efficiently because they have more patches (different types) to colonize.

Figure 12 illustrates the scenario, in which the asymmetricity of the environment enables the evolutionary branching of dispersal propensity in a metapopulation utilizing the slightly biased singular generalist strategy that is evolutionarily attracting in a monomorphic population. In figure 12, the environment consists of unequal amount of two patch types with swapped carrying capacities. An unbiased generalist observes no differences between such patches, and hence evolutionary branching of the dispersal propensity is not possible in a metapopulation using the unbiased generalist strategy. Due to the asymmetricity, the singular specialization strategy is, however, sufficiently distant from the unbiased strategy in order to enable evolutionary branching of the dispersal propensity. In Figure 12, one actually observes two successive events of evolutionary branching of dispersal. In both cases, the dispersal propensity at the branching point is rather large. Therefore, the dispersal propensity of one of the emerging morphs cannot increase much more and this morph remains nearly generalist, while the dispersal propensity of the other emerging morph decreases substantially. During the first event of evolutionary branching, the morph with decreasing dispersal propensity specializes in the less abundant resource 1 ($s = 1$), whereas during the second evolutionary branching the newly appeared morph with decreasing dispersal propensity specializes in the more abundant resource ($s = 0$). Finally, the metapopulation reaches a trimorphic state comprised of one abundantly dispersing generalist and two scarcely dispersing specialists. The exploited niches are qualitatively similar to those in the case involving symmetric environments (Figure 11).

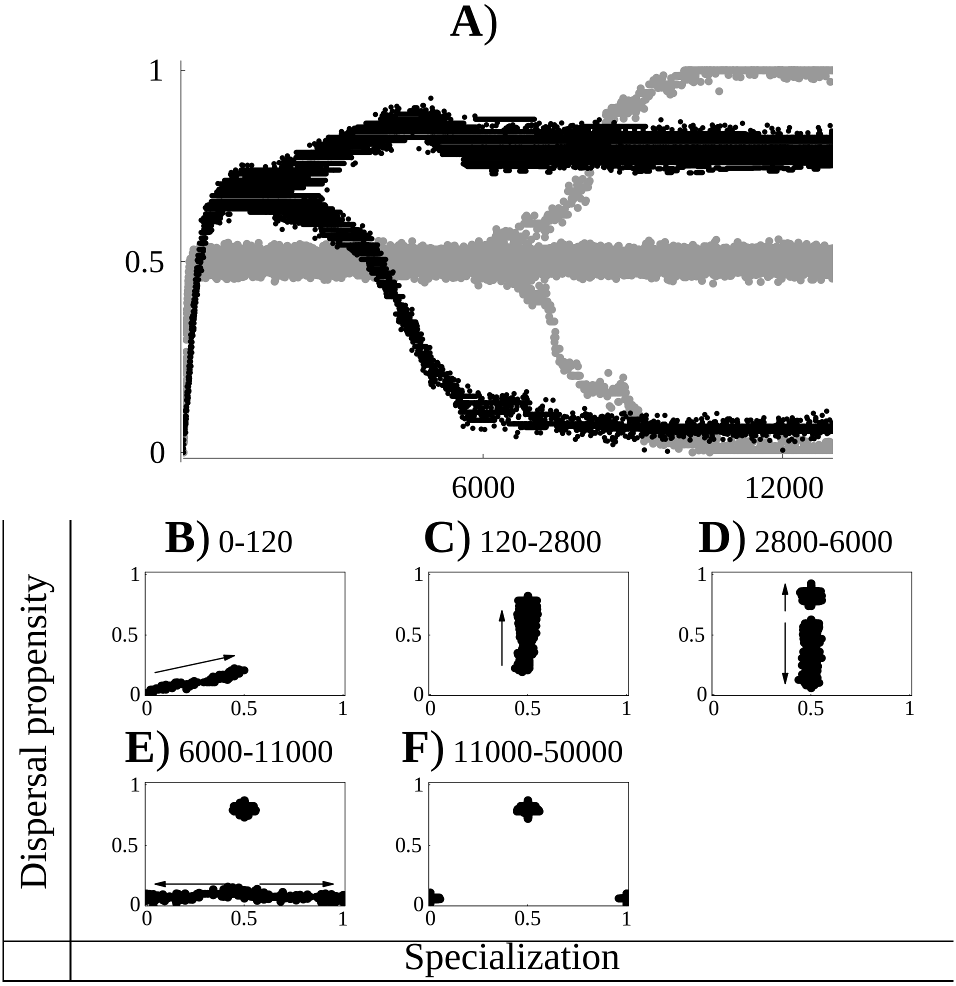

Figure 10: Panel A illustrates the strategies present in the metapopulation with local dynamics of the Beverton–Holt type as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e. Each dot in Panels B-F represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s. The arrows in Panels B-F indicate the direction of evolution. The initial strategy $(e, s) = (0.1, 0.1)$. The simulation ended in a trimorphic metapopulation using strategies $(e, s) \approx (0.1, 0)$, $(0.1, 1)$ and $(0.8, 0.5)$. Parameter values: $\theta = 0.1$, $\pi = 0.99$, $\lambda = 3$, $c = 0.05$, $K_1^1 = 5$, $K_2^1 = 1$, $K_1^2 = 1$, $K_2^2 = 5$, $K_1^3 = K_2^3 = 1$, $p_1 = p_2 = 0.25$, $p_3 = 0.5$

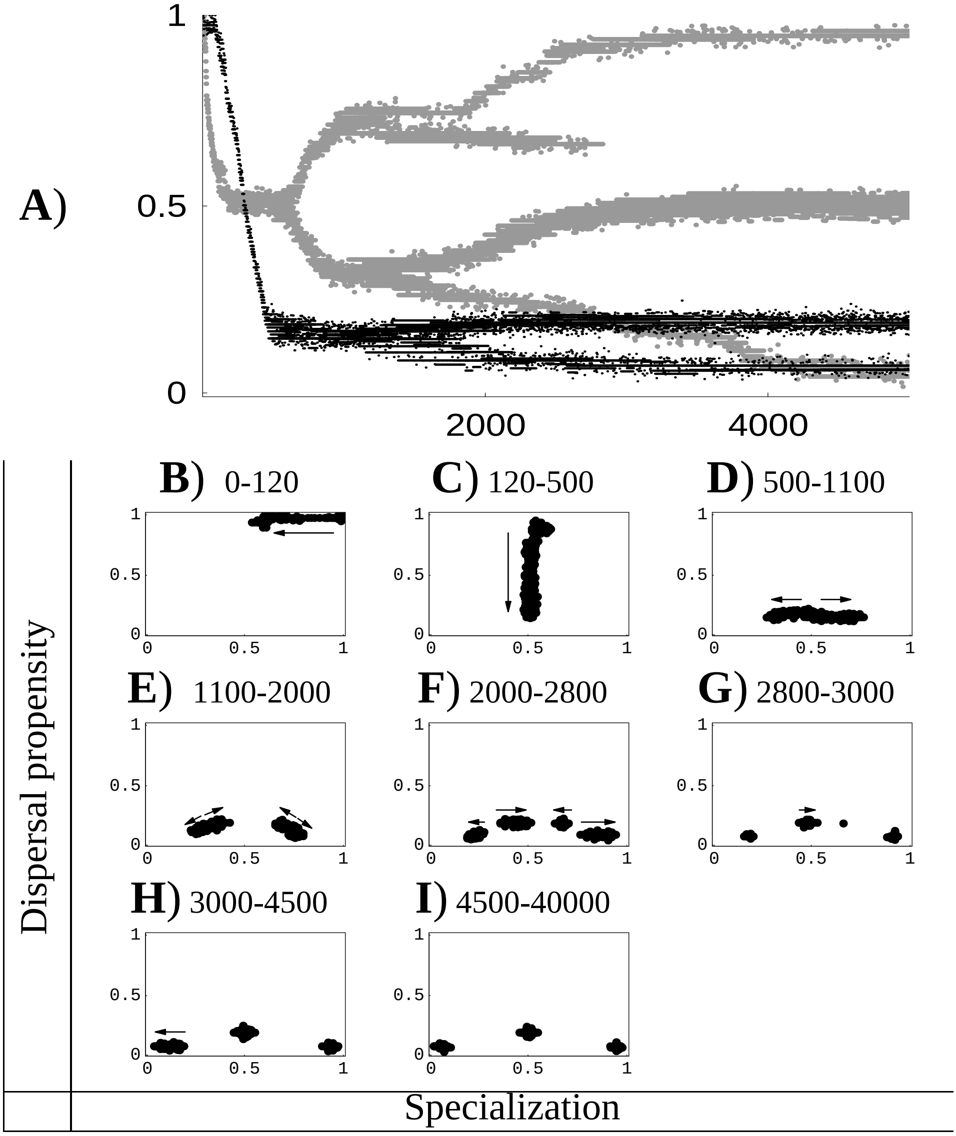

Figure 11: Panel A illustrates the strategies present in the metapopulation with local dynamics of the Beverton–Holt type as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e. Each dot in Panels B-I represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s. The arrows in Panels B-I indicate the direction of evolution. The initial strategy $(e, s) = (1, 1)$. The simulation ended in a trimorphic population using strategies $(e, s) \approx (0.2, 0.5)$, $(0.1, 0.1)$ and $(0.1, 0.9)$. Parameter values: $\theta = 0.1,\ \pi = 0.8,\ \lambda = 3,\ c = 0.05,\ K_1^1 = K_2^2 = 3,\ K_1^2 = K_2^1 = 1,\ p_1 = p_2 = 0.5$

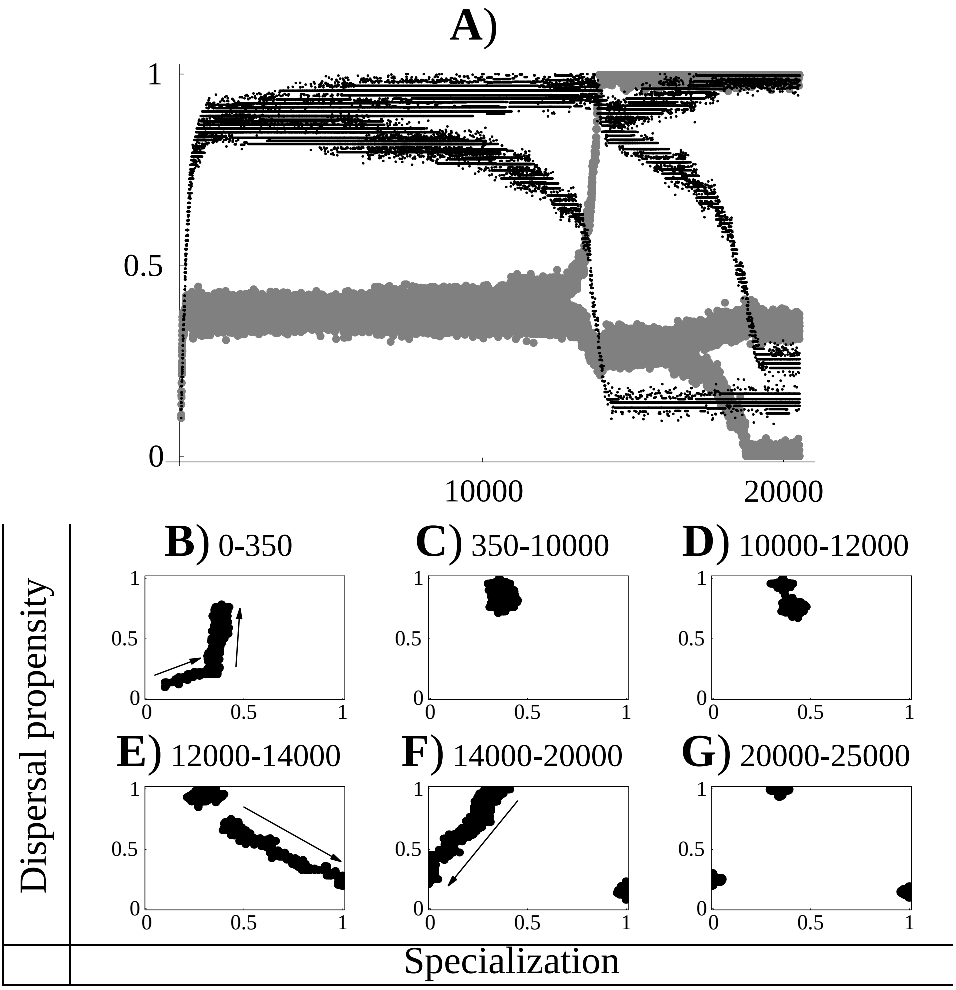

Figure 12: Panel A illustrates the strategies present in the metapopulation with local dynamics of the Beverton–Holt type as a function of evolutionary time. Grey curve = the specialization component s of the strategy, black curve = the dispersal component e. Each dot in Panels B-G represents a strategy that has been present in the metapopulation during the corresponding evolutionary time interval. The vertical axis illustrates the dispersal propensity e and the horizontal axis illustrates specialization s. The arrows in Panels B-G indicate the direction of evolution. The initial strategy $(e, s) = (0.1, 0.1)$. The simulation ended in a trimorphic population using strategies $(e, s) \approx (0.25, 0)$, $(1, 0.4)$ and $(0.1, 1)$. Parameter values: $c = 0.1$, $\pi = 0.99$, $\theta = 0.1$, $\lambda = 1.5$, $K_1^1 = K_2^2 = 10$, $K_1^2 = K_2^1 = 1$, $p_1 = 0.2$, $p_2 = 0.8$.

Evolutionary effects of ecological parameters

In this thesis, the evolutionary dynamics of specialization are dominated by the trade-off parameter θ. For low values of θ, the evolutionary dynamics of specialization always converge to a specialist strategy. As θ increases, the generalist strategy first turns from an evolutionary repellor into a branching point. For even greater values of θ the generalist strategy becomes an evolutionary endpoint, after which increasing θ does not cause any further qualitative changes under equilibrium ecological dynamics (when evolutionary suicide is not possible). Thus, there are always at least two critical values of θ:

- At θ_1^*, the generalist strategy turns from an evolutionary repellor into a branching point.
- At θ_2^*, the generalist strategy turns from a branching point into an evolutionary endpoint (ESS)

Since the trade-off parameter θ measures the additional benefit or cost of generalism (see equation (20)), the critical values of θ can be exploited when studying how changes in different ecological parameters affect the evolutionary dynamics of specialization. If a certain change in ecological parameters causes both of the critical values to decrease, this change can be interpreted to favor the spread of the generalist strategy. Correspondingly, a change that causes an increase in both critical values favors the spread of the specialist strategies. If θ_1^* decreases and θ_2^* increases, the parameter domain where evolutionary branching occurs becomes larger.

Nurmi and Parvinen (2008) did this kind of investigation for a variety of different metapopulation models assuming constant dispersal propensity, whereas Nurmi and Parvinen (2011) assumed the dispersal propensity always to have the corresponding evolutionarily singular value. Both studies focused on metapopulations where within-patch dynamics have fixed-point attractors. The results of Nurmi and Parvinen (2008) and Nurmi and Parvinen (2011) are qualitatively similar concerning the following conclusions:

- Increasing environmental heterogeneity, i.e., increasing difference between the resource carrying capacities K_1 and K_2 among the patches enlarges the parameter domain where evolutionary branching may occur.

- Increasing fecundity λ and increasing dispersal survival π favor the spread of the generalist strategy. In the case of joint evolution (Nurmi and Parvinen, 2011), this is natural, since also the singular dispersal propensity increases, which again is natural since, on one hand, increasing dispersal survival obviously increases dispersal propensity, and on the other hand, increasing fecundity increases crowding within the patches, which makes dispersal more profitable. More surprising is the observation that increasing fecundity favors the spread of the generalist strategy even with constant dispersal propensity (Nurmi and Parvinen, 2008).

Nurmi and Parvinen (2008) observed, that with constant dispersal propensity, the evolutionary effects of decreasing catastrophe probability depend on the details of the within-patch dynamics. However, Nurmi and Parvinen (2011) deduced that decreasing catastrophe probability always results in decreasing dispersal propensity, which always enlarges the parameter domain where evolutionary branching may occur.

Clonal interference and the joint evolution of dispersal propensity and specialization

Besides, the results described above, Nurmi and Parvinen (2011) demonstrated that the evolution of dispersal is usually slower than the evolution of specialization, i.e., evolutionary forces influencing specialization are stronger than those influencing dispersal. This phenomenon is rather natural, since the degree of specialization always affects reproduction. Dispersal affects both the reproduction of the dispersers and the reproduction of those remaining. However, the effect on the dispersers' fecundity depends crucially on how the original patch and the target patch differ in terms of quality and crowdedness. Thus, it requires several generations and dispersal events to be able to observe the average effect of dispersal on the dispersers' fecundity. Moreover, the fecundity of the remaining individuals is increased by dispersals only in crowded patches.

When two traits are evolving and there are significant differences in the strength of the evolutionary forces influencing them, it is even possible that the evolution of the faster evolving trait slows down or halts the evolution of the other. For example, in Figures 10, 11 and 12 the evolution of specialization halts the evolution of dispersal at the initial phase. This may occur, since mutations affect only one trait at a time (no pleiotropy). When a new mutant dispersal propensity comes up, it has initially a very small population size that increases rather slowly even if the mutant is capable to invade the population. New mutants usually come up before this mutant population has reached a significant size. Consequently, the new mutants usually have a dispersal propensity inherited from the initial resident population. If any of these mutants has a specialization strategy that is capable to invade the resident, this mutant (carrying the original dispersal propensity) will increase rapidly in population size (due to the stronger evolutionary forces) and outcompete the other strategies, including the one in which the new dispersal propensity results in higher invasion fitness compared to the initial resident population.

This phenomenon is based on clonal interference. It is possible, since there is no pleiotropy or recombination (Gerrish and Lenski, 1998). In this thesis, pleiotropy is not under consideration, since already the case without pleiotropy involves the main evolutionary feature the search of which motivated the analysis of the joint evolution of dispersal propensity and specialization: the evolutionary attainability of the trimorphic coexistence of a generalist strategy with two specialist strategies.

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