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**MATHEMATICS
INSPIRED BY DARWIN**

**Adaptive dynamics of
dispersal and cooperation**

by

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Abstract

In 1859, Charles Darwin published his theory of evolution by natural selection, the process occurring based on fitness benefits and fitness costs at the individual level. Traditionally, evolution has been investigated by biologists, but it has induced mathematical approaches, too. For example, adaptive dynamics has proven to be a very applicable framework to the purpose. Its core concept is the invasion fitness, the sign of which tells whether a mutant phenotype can invade the prevalent phenotype. In this thesis, four real-world applications on evolutionary questions are provided. Inspiration for the first two studies arose from a cold-adapted species, American pika. First, it is studied how the global climate change may affect the evolution of dispersal and viability of pika metapopulations. Based on the results gained here, it is shown that the evolution of dispersal can result in extinction and indeed, evolution of dispersal should be incorporated into the viability analysis of species living in fragmented habitats. The second study is focused on the evolution of density-dependent dispersal in metapopulations with small habitat patches. It resulted a very surprising unintuitive evolutionary phenomenon, how a non-monotone density-dependent dispersal may evolve. Cooperation is surprisingly common in many levels of life, despite of its obvious vulnerability to selfish cheating. This motivated two applications. First, it is shown that density-dependent cooperative investment can evolve to have a qualitatively different, monotone or non-monotone, form depending on modelling details. The last study investigates the evolution of investing into two public-goods resources. The results suggest one general path by which labour division can arise via evolutionary branching. In addition to applications, two novel methodological derivations of fitness measures in structured metapopulations are given.

Tiivistelmä

Vuonna 1859 Charles Darwin julkaisi teorian luonnonvalinnan kautta tapahtuvasta evoluutiosta, joka prosessina perustuu yksilöiden kokemuksiin kelpoisuusetuihin ja -haittoihin. Perinteisesti evoluutiota ovat tutkineet biologit, mutta sitä voidaan tutkia myös matemaattisesti. Esimerkiksi adaptiivinen dynamiikka on osoittautunut erittäin käyttökelpoiseksi tähän tarkoitukseen. Adaptiivisen dynamiikan keskeisin käsite on kelpoisuus. Kelpoisuuden merkki kertoo, pystyykö aluksi pieni mutanttipopulaatio kasvamaan ja mahdollisesti syrjäyttämään vallitsevan populaation. Tässä väitöskirjassa on esitetty neljä reaalimaailman sovellusta evolutiivisista kysymyksistä. Innoitus kahteen ensimmäiseen tutkimukseen saatiin kylmiin oloihin sopeutuneesta Amerikan piiskujäniksestä. Ensimmäisessä työssä tarkasteltiin, miten ilmastonmuutos voi vaikuttaa muuttoliikkeen evoluutioon ja piiskujänismetapopulaation elinkykyyn. Tulosten perusteella voidaan sanoa, että muuttoliikkeen evoluutio voi johtaa sukupuuttoon. Tämä tulisi ottaa huomioon, kun arvioidaan sirpaloituneissa elinympäristöissä elävien lajien elinkelpoisuutta. Toinen tutkimus keskittyi populaatiotiheydestä riippuvan muuttoliikkeen evoluutioon pienilaikkuisessa metapopulaatiossa. Tuloksena oli varsin yllättävä epäintuitiivinen ilmiö, jossa populaatiotiheydestä riippuva muuttoliike voi kehittyä epämonotoniseen muotoon. Yhteistyö on yleistä monella elämän tasolla huolimatta siitä, että se on alttiina itsekkäiden huijareiden hyväksikäytölle. Tämä motivoi kahta viimeistä sovellusta, joista ensimmäinen koskee yhteistyön evoluutiota. Työssä näytetään, miten populaatiotiheydestä riippuva yhteistyö voi kehittyä kvalitatiivisesti erilaiseen muotoon, monotoniseen tai epämonotoniseen muotoon, riippuen mallinnuksen yksityiskohdista. Viimeisessä tutkimuksessa tarkastellaan kahden julkishyödykeressurssin tuottamisen evoluutiota. Tulokset osoittavat yleisen tavan, miten työnjako voi kehittyä evolutiivisen haarautumisen kautta. Lisäksi väitöskirjassa on johdettu kaksi uutta menetelmää kelpoisuuden laskemiseksi rakenteisissa metapopulaatioissa.

Theses

With the knowledge gathered during this thesis project the claims below are being set.

- Evolution of dispersal should be incorporated into the viability analysis of species living in fragmented habitat.
- In a changing environment, evolution of dispersal may drive vulnerable species to extinction or save them.
- Density-dependent dispersal may evolve to a non-monotone state. Thus, one should be cautious when building models, in which monotone density-dependent dispersal is preassumed.
- Contradicting the intuition, density-dependent cooperation may evolve to a hump-shaped form.
- Modelling details may have a significant impact on qualitative results obtained.
- Labour division can emerge due to evolution by natural selection in a public-goods game with two resources.
- Nature provides a huge variety of evolutionary questions that can be studied mathematically, and in specific with adaptive dynamics.

List of original publications

1. Anne Seppänen, Kalle Parvinen and John D. Nagy. 2012.
Evolution of dispersal in American pika (*Ochotona princeps*) meta-populations.
Evolutionary Ecology Research, **14**:1-29.
2. Kalle Parvinen, Anne Seppänen and John D. Nagy. 2012.
Evolution of complex density-dependent dispersal strategies.
Bulletin of Mathematical Biology, **74**:2622-2649.
3. Kalle Parvinen and Anne Seppänen.
On fitness in metapopulations that are both size- and stage-structured.
Submitted.
4. Anne Seppänen and Kalle Parvinen.
Evolution of density-dependent cooperation.
Submitted.
5. Anne Seppänen, Kalle Parvinen and John D. Nagy.
Rich evolutionary dynamics in a public-goods game with two resources.
Submitted.

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Part I

General Theory

Chapter 1

Introduction

Charles Darwin published his theory on evolution by natural selection in 1859 (Darwin, 1859). Today, we understand that evolution not only interweaves with ecology everywhere, but it will also continue as long as life exists. Selectional pressures are always present. Furthermore, evolutionary processes occur in multiple levels, from genes and cells, organisms like plants and animals, to social structures. Eventually, in process of time, Darwin and his theory have got the acknowledgement deserved. Only, Alfred Russel Wallace and his contribution (e.g., Wallace, 1855) into evolution theory is often left in a shadow. Later, Darwin's evolution theory, Mendelian genetics and systematics were joined in a modern evolutionary synthesis generated by many evolutionary biologists, including Ernst Mayr (Mayr, 1942) and Ronald Fisher (Fisher, 1930). However, still not everyone accepts the theory.

The theory of evolution by natural selection is rather simple. It is based on only few assumptions. Individuals have a phenotype, which affects their survival or reproductive success. Phenotypes, or traits, are inheritable. In a population there is variation of phenotypes, i.e. individuals are different. Furthermore, individuals reproduce on average more than just to replace themselves. Due to limited resources, individuals struggle for their survival and not everyone manages to reproduce before dying. The most fitted individuals in the present environment are able to survive better and to produce on average more offspring than other individuals. This leads to a change in the phenotype frequencies as well as in the trait frequencies within the population. This process is known as adaptation. Although evolution by natural selection can be observed as a change in phenotype frequencies at the population level, the actual process occurs at the individual level based on the fitness benefits and fitness costs of the individual.

Understanding evolution and its numerous levels affects how we conceptualize the world around us, and ourselves as part of the world. Thus, it is important to comprehend and to obtain more knowledge on evolution. This is especially true when new selection pressures are introduced by man (e.g., Palumbi, 2001). That occurs often unintentionally. For example pesticide use or drug treatment can select for resistant strains of pests or pathogens.

Although evolution might be perceived as a research field for biologists, it can be, and indeed, it has been studied also mathematically. For example, adaptive dynamics (Metz et al., 1996; Geritz et al., 1997, 1998) has proven to be a very applicable and powerful framework for the purpose. Mathematical modelling can provide general insights on ecological and evolutionary processes and reveal unintuitive phenomena, which might be left in obscure otherwise. Theoretical approaches become especially important, when experimental studies are enormously difficult or costly to be realized, or when such studies are totally impossible or unethical to execute.

In the next chapter (Chapter 2), first, different approaches to model population dynamics are described. Second, a concept of a metapopulation is explained, i.e., how local populations can be connected via migration. Third, adaptive dynamics and its basic concepts are presented. In the subsequent chapter (Chapter 3), the main results of the attached original articles and manuscripts are covered.

Chapter 2

Methods

The evolutionary play takes place in the ecological theatre (Hutchinson, 1965). Obviously, the scenery must be well described to be able to follow the act. However, there is no manuscript for the actual play. What occurs depends always on many factors and especially, what kind of mutant phenotypes appear, i.e., which actors are present in each scene. In specific, evolution by natural selection is shaped by the fitness benefits and fitness costs of the individuals present. That implies that the ecological model for the population dynamics needs to incorporate the essential characteristics of the individuals constituting the population.

In this chapter different approaches to build a scenery, i.e., to model population dynamics are described. A concept of a metapopulation, how local populations can be connected via migration, is introduced. Eventually, the core idea of the evolutionary play is explained. That is, the framework of adaptive dynamics and its basic concepts are presented.

2.1 Population dynamics

Mathematical models try to capture the main features of the system they are to describe. It is not always obvious what to include and what to exclude. Certainly, a model should not be as complex as the real-world system. The more complicated model, the more difficult it will be to analyse. Furthermore, results gained from a simplified model might provide more general interpretations, and more insightful aspects of the system. Indeed, modellers are always balancing between real world complexity and mathematical tractability.

Population models can be categorized at least in three different ways. First, phenomenological and mechanistic models, second, continuous and discrete time models, and third, deterministic and stochastic models.

A phenomenological model contains characteristics of a population, but most often lacks interpretation on the individual-level processes. On the contrary, a mechanistic model (Schoener, 1986) is derived from the assumptions on individuals and their processes, e.g., birth and death events, that occur at a very basic level. As we know, natural selection occurs at the individual level instead of a group or a population level. Therefore, when asking evolutionary questions, it is essential that the population dynamics are derived from the first principles (Geritz and Kisdi, 2012), i.e., from individual level processes. However, compared to phenomenological models, mechanistic models often turn out to be much more complex and more difficult to investigate analytically or even numerically.

Population models can be categorized based on different approaches with respect to time, such as continuous-time and discrete-time models. The features of reproduction or breeding season dynamics often determine the type of the model. Here, models defined in discrete-time, in continuous-time and in semi-discrete time are introduced.

Many population models are described with a system of differential equations and initial values. Such models are deterministic. The word deterministic refers that the state of the system can be determined at any time in a future, if its state is known at least in one time point. However, the world is rather stochastic in nature. Stochasticity can be included into the population models too, for example by using Markov chains or other stochastic processes.

2.1.1 Discrete-time population dynamics

Consider individuals within a population, which breed only at a certain time of year or only once in some other major period of time. Then, a natural way to describe the population dynamics would be a difference equation, a discrete time model

$$N_{t+1} = f(N_t) \tag{2.1}$$

where N_t is the population size (density) at time t and the function $f(N)$ describes the population growth depending on the population size. It is often assumed that $N_t \in \mathbf{R}^n$.

One famous discrete-time model is from 1202 by Leonardo Pisano, commonly known as Fibonacci (Sigler, 2002). He modelled reproducing rabbit pairs with a mechanistic approach (see Table 2.1). Assume that rabbits are born as juveniles. Juveniles mature to become adults in one time step. A pair of adult rabbits reproduces for ever and gets two offspring (one pair) in each time step. Initially, there is a newborn rabbit

pair at time $t = 0$. It matures and becomes an adult pair at time $t = 1$. Then the adult rabbit pair reproduces. There will be the adult pair and a newborn pair at time $t = 2$. The first adult pair reproduces again and the newborn pair matures and becomes an adult pair. Hence, at time $t = 3$ there are two adult pairs and one newborn pair. The process continues similarly, see Table 2.1.

Table 2.1: Mechanistic model by Fibonacci.

time	adult pairs	newborn pairs	total pairs
0	0	1	1
1	1	0	1
2	1	1	2
3	2	1	3
4	3	2	5
5	5	3	8
6	8	5	13
\vdots	\vdots	\vdots	\vdots

The initial population sizes counted in rabbit pairs at time $t = 0$ and $t = 1$ are obviously equal to one, $N_0 = N_1 = 1$. The total population size $N_{t+1} = A_{t+1} + J_{t+1}$. Since $A_{t+1} = N_t$ and $J_{t+1} = A_t$, the following recursion is obtained

$$N_{t+1} = N_t + N_{t-1}, \quad \text{for } t = 1, 2, 3, \dots \quad (2.2)$$

The model results in the Fibonacci sequence 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, ...

2.1.2 Continuous-time population dynamics

Consider individuals within a population, which have no special breeding season. Individuals can breed at any time of a year. This is true for many species, e.g., for humans as well as for yeasts. Time as such does not affect the dynamics, only population size matters. Then, population dynamics are autonomous, and can be described by a continuous-time model. In practice this often means a (system of) differential equation(s)

$$\frac{dN(t)}{dt} = f(N), \quad (2.3)$$

where $N(t) \in \mathbf{R}^n$ is the vector of population densities at time t and the function f represents the growth rate. Continuous-time models are widely

used. One famous example is the logistic growth model

$$\frac{dN(t)}{dt} = rN \left(1 - \frac{N}{K} \right), \quad (2.4)$$

where r is the intrinsic growth rate and K is the carrying capacity. Note, that written like this, the logistic model is phenomenological. However, a similar form of the model can be derived with the mechanistic approach too (Geritz and Kisdi, 2012). Then, the model parameters obviously stand for different characteristics.

Referring to one of the model derivations (e.g., Geritz and Kisdi, 2012), let us assume, that there are M sites, e.g., territories. With a population size N , the proportion of empty sites is $1 - N/M$. Birth can occur only into empty sites, or alternatively, an offspring landing on an occupied site dies. Birth and death per capita rates are β and μ , respectively. Then, population dynamics follow

$$\frac{dN(t)}{dt} = \beta N(1 - N/M) - \mu N. \quad (2.5)$$

This is the logistic equation, if we substitute $r = \beta - \mu$ and $K = \frac{\beta - \mu}{\beta} M$.

2.1.3 Semi-discrete-time population dynamics

Naturally, breeding hardly ever occurs strictly in a discrete or in a continuous manner in time. Furthermore, there might be other significant processes, which should be incorporated into the model, and which change along the year. Such processes could include resource availability or survival due to weather conditions. Therefore, a compromise between the two extreme types of modelling might be an appropriate approach. Following Ghosh and Pugliese (2004), Pachepsky et al. (2008) and Singh and Nisbet (2007), we call such intermediate form of models with the name “semi-discrete”.

Consider individuals within a population experiencing a sequence of “phases” or seasons throughout the year in which the population dynamical forces vary. Time within a year (or any other major period, e.g., census period) is measured by $\tau \in [0, 1]$. A population census occurs at the beginning of each year ($\tau = 0$). Within each season, the population experiences a more-or-less fixed constellation of forces, but the set of forces changes at discrete points of time. The boundaries between behavioural “seasons” are marked by τ_i , $0 < \tau_1 < \tau_2 < \dots < 1$. Within-season dynamics are governed by a system of differential equations, a continuous time model. The initial value for each season dynamics is calculated using the

end value from the previous season dynamics by another set of equations. These are the discrete (instant) events (e.g. birth) connecting different seasons (Geritz and Kisdi 2004, see also Eskola and Geritz, 2007; Eskola and Parvinen, 2007, 2010).

The above description becomes clear in the next example. Time within a year is denoted by τ , and years by t . Consider a population consisting of adults A and juveniles J . Breeding occurs at time $\tau = 0$. The initial values for adults and juveniles are then

$$\begin{cases} A_{t+1}(0) &= A_t(1) \\ J_{t+1}(0) &= f(A_{t+1}(0))A_{t+1}(0) \end{cases} \quad (2.6)$$

We may assume $A_0(0) = A_0$ for the very first breeding event in the population. All individuals suffer from natural mortality. In addition, there is interference between juveniles before they mature. Then, the population dynamics follow

$$\begin{cases} \frac{dA(\tau)}{d\tau} &= -\mu A \\ \frac{dJ(\tau)}{d\tau} &= -\mu J - iJ^2 \end{cases} \quad (2.7)$$

Juveniles mature and become adults at time τ_1 . Thus, we write

$$\begin{cases} A(\tau_1) &= A(\tau_1-) + J(\tau_1-) \\ J(\tau_1) &= 0 \end{cases} \quad (2.8)$$

For the rest of the year adults still suffer from mortality

$$\frac{dA(\tau)}{d\tau} = -\mu A. \quad (2.9)$$

The next breeding event occurs in the beginning of the next year according to (2.6).

2.2 Metapopulation dynamics

A metapopulation is an assemblage of local populations connected via migration. The first mathematical metapopulation model was introduced by Levins (1969, 1970). He described the dynamics of the fraction of occupied habitat patches P based on local population extinctions c and recolonizations b

$$\dot{P} = bP(1 - P) - cP. \quad (2.10)$$

Levins (1969) showed that the metapopulation can persist only if the recolonization rate exceeds the extinction rate. Hence, dispersal or migration between patches is a key feature in the survival of a metapopulation.

Even though the Levins' classical model ignored the local population dynamics, it has provided an important conceptual base on the future progress of the metapopulation theory (e.g., Hanski and Gilpin, 1997; Hanski, 1999; Hanski and Gaggiotti, 2004; Gyllenberg and Hanski, 1992; Gyllenberg et al., 1997; Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001; Parvinen and Metz, 2008). It is not surprising that the metapopulation setting is receiving ever more attention as anthropogenic alteration accelerate around the world and an increasing number of species suffer from habitat fragmentation.

2.3 Evolution and adaptive dynamics

The word *evolution* is often associated with Charles Darwin, who wrote the famous, and in the beginning controversial, theory on evolution by natural selection (Darwin, 1859). Later, on 20th century Ernst Mayr and Ronald Fisher among many others had an enormous influence on the conceptual understanding of evolution (e.g., Mayr, 1942, 1963; Fisher, 1930).

Evolution by natural selection involves variation in individual's phenotypes. Phenotypes are heritable and affect individual's survival or reproductive success. Individuals produce more offspring than necessary just to replace themselves. Due to the resource or other limitations all of them cannot survive until reproductive age. This leads to a struggle for existence, i.e., natural selection. Over the time, proportions of phenotypes in the population change. In time, the fittest outcompete other types leading to adaptation.

Fitness benefits and fitness costs experienced by the individuals shape the path of evolution for all phenotypic traits. Especially in the past, there has been lot of debate on what level selection actually acts, between the populations (e.g., Wynne-Edwards, 1962, 1963) or between the individuals within a population (e.g., Williams, 1966; Maynard Smith, 1964). In general, it is now accepted that it is the fitness of an individual that matters. However, there are still some intriguing questions related to major transitions in evolution (Maynard Smith and Szathmáry, 1995), in which a new level of individuality originates. Indeed, the transitions are often difficult to explain purely due to the fitness benefits on the lower level of individuality (Michod and Roze, 2001) and group selection seems to be a tempting reasoning.

There exist several methods to study evolutionary questions, e.g., population genetics (e.g., Fisher, 1930; Wright, 1931), quantitative genetics (e.g., Hardy, 1998), adaptive dynamics (e.g., Metz et al., 1996) and many different kinds of simulations, (e.g., Gerisch and Chaplain, 2008).

Within this thesis project, the studies have focused only on the methodology of adaptive dynamics. Indeed, the framework of adaptive dynamics (Metz et al., 1996; Geritz et al., 1997, 1998) has grown to a large set of tools to study evolution and it has been applied for a broad range of evolutionary questions. However, for future perspectives it would be worth of effort to combine the knowledge achieved by different approaches and to build a new synthesis to increase evolutionary understanding. Such early steps have already been taken (e.g., Priklopil, 2012).

One question in evolutionary dynamics is the following: can a mutant with the strategy s_{mut} invade the resident with the strategy s_{res} . To answer the question, Metz et al. (1992) defined the invasion fitness as the long-term exponential growth rate r of a rare mutant in the environment set by the resident. A positive invasion fitness implies that the initially small mutant population is able to grow and possibly replace the resident. However, it does not imply, that replacement will happen, only that it is possible. First, the mutant population is assumed to be initially very small. Therefore, it may disappear simply due to demographic stochasticity. Second, even though the mutant population may increase in the beginning, the coexistence of the mutant and the resident is a possible outcome. Third, if the resident has multiple population-dynamical attractors, it is possible that the "resident strikes back" (Mylius and Diekmann, 2001) the mutant that has successfully started to invade. The population dynamics may lead to an alternative attractor of the resident, in which the invasion fitness of the mutant is negative and it cannot invade anymore.

In adaptive dynamics a few fundamental assumptions are made. First, the resident or residents are on their population-dynamical equilibrium or attractor when a new mutant appears. Second, mutational steps are random and small, but not infinitesimally small. That means that a new mutant phenotype differs only slightly from one of the prevalent phenotypes. Third, the mutant population is initially very small compared to the prevalent residents' populations. That is, a mutant population has initially no effect on residents' population dynamics, neither directly nor indirectly, e.g., via environmental effects such as resource usage. Later, when and if, the mutant population has grown bigger it does have an effect on the resident's population dynamics.

Adaptive dynamics take an advantage of the time scale separation method. That refers to the first assumption above, mutations occurring so infrequently that the residents have reached their population dynamical attractor whenever a new mutation occurs. Thus, slower evolutionary dynamics run on top of faster population dynamics. In practice, the invasion fitness of a mutant is obtained in the environment where the residents are

on their population dynamical attractor. Here, also clonal reproduction is assumed. That assumption can be relaxed (Parvinen and Metz, 2008), especially if the biological question requires sexual reproduction.

One may observe nature full of amazing adaptations. Indeed, researchers have investigated evolutionary questions on many traits. Especially, in metapopulation setting, the traits such as dispersal (Parvinen, 1999; Metz and Gyllenberg, 2001; Gyllenberg and Metz, 2001; Gyllenberg et al., 2002; Parvinen, 2006), local adaptation (Kisdi, 2002), specialization (Parvinen and Egas, 2004; Nurmi et al., 2008; Nurmi and Parvinen, 2008), reproductive effort (Ronce et al., 2000) and cooperation (Parvinen, 2011, 2013) have been studied.

2.3.1 Inclusive fitness

A notation that kin effects can shape the evolution led to a modelling concept of inclusive fitness (Hamilton, 1964a,b). Inclusive fitness is a biased sum of direct and indirect fitness benefits of the focal individual. More precisely,

$$\text{inclusive fitness} = \text{direct fitness} + \text{relatedness} \cdot \text{indirect fitness}.$$

The concept has provided great insight especially to the evolution of altruistic behaviour, explaining that it is not only individuals own success that matters, but in the presence of related individuals their fitness benefits contribute too (Ferrière and Michod, 2011).

According to the famous Hamilton's rule (Hamilton, 1964a,b) altruistic cooperation can evolve if $R_g \cdot B > C$, where R_g is the genetic relatedness of the recipient to the actor, B is the additional reproductive benefit gained by the recipient of the altruistic act, and C is the reproductive cost to the individual performing the act. Note, that $-C$ corresponds to the direct benefits in the inclusive fitness formulation. The Hamilton's rule has been extended and applied in multiple studies (e.g., Smith et al., 2010), for a review see West et al. (2002).

Hamilton and May (1977) showed that also dispersal can be understood as altruistic trait that allows to avoid competition among relatives. For example, Gandon (1999) has applied inclusive fitness to investigate the evolution of dispersal. Although not all researchers agree with the concept of inclusive fitness (Nowak et al., 2010), it is broadly accepted (Abbot et al., 2011; Boomsma et al., 2011; Strassmann et al., 2011; Ferrière and Michod, 2011; Herre and Wcislo, 2011). Furthermore, its leading idea is linked to the unifying concept of invasion fitness (Metz et al., 1992).

2.3.2 Invasion fitness

To study evolutionary dynamics with the framework of adaptive dynamics, there is the special concept of invasion fitness. Invasion fitness is used to answer the question, whether a mutant may or may not invade the resident. Invasion fitness of a rare mutant is its long-term exponential growth rate in the environment E_{res} set by the resident (or residents) population(s) (Metz et al., 1992). We denote this fitness

$$r(s_{\text{mut}}, E_{\text{res}}), \quad (2.11)$$

where s_{mut} is the strategy of the mutant.

If the actual invasion fitness is difficult to calculate, the basic reproduction ratio $R(s_{\text{mut}}, E_{\text{res}})$ can be practical and appropriate to use as a proxy (Roughgarden, 1976; Diekmann et al., 1990). It is the expected number of surviving offspring of a typical or an average mutant individual in the population. The two measures, r and R , are connected via the natural logarithm, so that r and $\ln(R)$ are sign equivalent (Mylius and Diekmann, 1995).

In metapopulation models it is convenient to use the metapopulation reproduction ratio (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) as a proxy for invasion fitness. The concept of R_{metapop} is a clear analogue to the basic reproduction ratio. Instead of traditional reproducing generations it operates on dispersing generations. We denote this metapopulation reproduction ratio

$$R_{\text{metapop}}(s_{\text{mut}}, E_{\text{res}}). \quad (2.12)$$

Naturally, invasion of a mutant population is possible only when

$$R_{\text{metapop}} > 1, \quad (2.13)$$

which is equivalent to the exponential growth rate $r > 0$.

In practice, we follow a mutant disperser immigrating from the dispersal pool onto a patch and initiating a new local clan. This clan consists of the immigrant itself and all of its lineal descendants produced on that patch until the clan is destroyed by local population extinction. Each surviving generation seeds the dispersal pool with new dispersers. Thus, the metapopulation reproduction ratio $R_{\text{metapop}}(s_{\text{mut}}, E_{\text{res}})$ is defined as the expected number of successful dispersers produced by an average local clan initiated by a mutant using a strategy s_{mut} in the environment E_{res} set by the resident.

Metz and Gyllenberg (2001) and Gyllenberg and Metz (2001) explain how to calculate the metapopulation reproduction ratio in various continuous-time metapopulation models. Parvinen (2006) presented an analogous method for discrete-time metapopulation models. In the original publication **I** it is explained how to extend these methods to a semi-discrete metapopulation model (Seppänen et al., 2012). The major methodological contribution presented in the original publication **III** involves a continuous-time metapopulation model, which is both size and stage structured, and how to obtain metapopulation reproduction ratio in a such generalized case (Parvinen and Seppänen, *subm*).

2.3.3 Singular strategies

The fitness gradient (selection gradient) tells the expected direction of evolution. For scalar strategies, the fitness gradient is defined as

$$G(s_{\text{res}}) = \left. \frac{\partial r(s_{\text{mut}}, E_{\text{res}})}{\partial s_{\text{mut}}} \right|_{s_{\text{mut}}=s_{\text{res}}},$$

where s_{mut} and s_{res} are the strategies of a mutant and the resident, respectively. Specifically, in one-dimensional strategy space and for small mutational steps, if the selection gradient is positive, invasion requires $s_{\text{mut}} > s_{\text{res}}$, and if the selection gradient is negative, invasion may occur only when $s_{\text{mut}} < s_{\text{res}}$. If mutations have larger phenotypic effects, this does not hold anymore.

For vector strategies the fitness gradient,

$$\mathbf{G}(\mathbf{s}_{\text{res}}) = (G_1(\mathbf{s}_{\text{res}}), G_2(\mathbf{s}_{\text{res}}), \dots, G_n(\mathbf{s}_{\text{res}})),$$

is a vector consisting of derivatives with respect to each strategy component:

$$G_i(\mathbf{s}_{\text{res}}) = \left. \frac{\partial r(s_{\text{mut},1}, \dots, s_{\text{mut},n}, E_{\text{res}})}{\partial s_{\text{mut},i}} \right|_{\mathbf{s}_{\text{mut}}=\mathbf{s}_{\text{res}}}.$$

Strategies for which the fitness gradient is zero are called evolutionary singular strategies (Geritz et al., 1997, 1998; Maynard Smith, 1976, 1982; Maynard Smith and Price, 1973; Christiansen, 1991; Eshel, 1983). Hence, such strategies s^* can be found by solving $G(s^*) = 0$. When the dimension of the strategy space is n , we have a system of n equations $G_i(s^*) = 0$, $i = 1, \dots, n$. For larger n , finding singular strategies becomes, in general, more demanding.

Evolutionary stability

If all mutants $s_{\text{mut}} \neq s^*$ have negative fitness, $r(s_{\text{mut}}, E_{\text{res}}) < 0$, or equivalently $R(s_{\text{mut}}, E_{\text{res}}) < 1$, no mutant strategy can invade and thus, the singular resident strategy s^* is uninvadable. Note, that the strategy s^* is a local fitness maximum. The singular strategy s^* is then called an evolutionarily stable strategy, or ESS (Maynard Smith, 1976, 1982; Maynard Smith and Price, 1973). Such a strategy is a possible endpoint of evolution.

When the strategy is one-dimensional, the local condition for the singular strategy s^* to be evolutionarily stable is

$$\frac{\partial^2 r(s_{\text{mut}}, E_{\text{res}})}{\partial s_{\text{mut}}^2} < 0 \quad (2.14)$$

In case the strategy space is multidimensional, the singular strategy \mathbf{s}^* is evolutionarily stable if the corresponding Hessian matrix of the invasion fitness is negative definite.

Convergence stability

The fact that a singular strategy is uninvadable does not necessarily imply that it would be evolutionarily attracting. A singular strategy is evolutionarily attracting if the repeated invasion of mutant strategies $s_{\text{mut}} \approx s_{\text{res}}$ into resident strategies s_{res} will lead to the convergence of resident strategies towards s^* (Christiansen, 1991). For one-dimensional strategies such convergence occurs if $G(s_{\text{res}}) < 0$ for $s_{\text{res}} > s^*$ and $G(s_{\text{res}}) > 0$ for $s_{\text{res}} < s^*$ at least when $s_{\text{res}} \approx s^*$. An equivalent condition is that $G'(s^*) < 0$. A monomorphically attracting singular strategy that is uninvadable, is called continuously stable strategy (Eshel, 1983). Such a singular strategy is also an evolutionary endpoint.

In a multidimensional case, convergence stability depends also on the mutational variance-covariance structure of the strategy components (Leimar, 2001). The canonical equation of adaptive dynamics can be written

$$\frac{d}{dt}\mathbf{s} = \frac{1}{2}\mu N_t \mathbf{B}(\mathbf{s}) \mathbf{G}(\mathbf{s}) \quad (2.15)$$

where μ denotes the mutation rate, N_t denotes the population density, the matrix \mathbf{B} denotes the process of generating variation in strategies through mutations, and \mathbf{G} is the selection gradient (Dieckmann and Law, 1996; Leimar, 2001). The matrix \mathbf{B} contains the variance of mutational effects in its diagonal and the covariance between the mutations in other elements. The partial derivative of the invasion fitness around the resident

trait value indicates how much the invasion fitness increases (or decreases) with a small mutational step in the corresponding component. That refers to the fitness gradient, which measures the quantity and the direction of selection, and hence, describes how fast or slowly evolution will change the corresponding strategies. Note, that higher variance increases the rate of evolution because it allows longer mutational steps. However, covariance between the mutations may change the evolutionary path, and hence affect also the convergence stability.

Evolutionary branching

A monomorphically evolutionarily attracting singular strategy is not necessarily an evolutionary endpoint. An evolutionarily attracting singular strategy can be beatable, i.e., it is not uninvadable. In that case, there are necessarily strategy pairs near the singular strategy, that are mutually invadable, and thus can coexist. Furthermore, the strategies of the dimorphic population start to diverge (see Fig. 2.3b). The singular strategy is thus dimorphically repelling, and is therefore called as a branching point. This holds, in specific, in one-dimensional strategy spaces, not in general. The branching point has to be reached before the actual diversification of strategies can take place. In a multidimensional strategy space it is again a matter of the variance-covariance structure whether the evolutionary branching can occur. For one-dimensional strategies, a complete classification of adaptive dynamics behaviours around singular strategies can be found in the article by Geritz et al. (1998).

Evolutionary suicide

Evolutionary suicide (Ferrière, 2000; Gyllenberg and Parvinen, 2001; Parvinen, 2002, 2005), also called Darwinian extinction (Webb, 2003) and evolution to extinction (Dieckmann et al., 1995), may occur when the selection gradient points out from a viability region. That is, evolution may first lead to a strategy which is just on the edge, where the population is still viable. However, a mutant with a strategy on the wrong side of the edge may be more fitted in the present environment, and thus, able to invade. By becoming the prevalent resident the mutant strategy drives the whole population to extinction. Such a strategy has been called also as a kamikaze mutant (Ferrière et al., 2004).

In order to evolutionary suicide to happen, there has to occur a bifurcation, where a non-extinct resident attractor disappears. Such transition can be either continuous or discontinuous. Consider first a continuous transition to extinction. On the boundary, where the transition occurs

the resident has a strategy s_{ext} , and its population size is zero. A mutant will then grow as it was in a virgin environment. This means, that exactly those mutants that are viable without the resident can invade. The mutants that are not viable cannot invade. Thus, the fitness gradient points into the viability region, not out, and evolutionary suicide is not possible. Therefore, a necessary condition for evolutionary suicide is that the transition to extinction is discontinuous (Gyllenberg and Parvinen, 2001).

2.3.4 Elucidation of evolutionary dynamics

There are numerous options to illustrate the evolutionary dynamics. Here, pairwise invasibility plots, bifurcation diagrams, trait substitution sequences and phase plane plots are shortly described.

Pairwise Invasibility Plot

In case the resident is monomorphic and the strategy is a scalar, the sign of the invasion fitness can be shown in a pairwise invasibility plot (PIP) (Matsuda, 1985; Van Tienderen and De Jong, 1986). This is fairly easy and illustrative way to represent the evolutionary outcome, e.g., Fig. 2.1. In a PIP, horizontal and vertical axes represent the strategies of the resident and of the mutant, respectively. In gray regions marked also with a plus sign the mutant strategy can invade, but in white regions with minus sign it cannot.

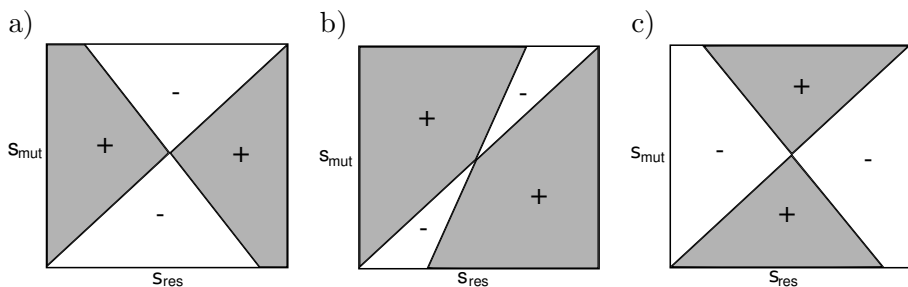


Figure 2.1: Pairwise Invasibility Plots, when the intersection of the isoclines is a) an evolutionary stable strategy, b) monomorphically attracting and dimorphically repelling, i.e. a branching point and c) a repelling singular strategy.

Evolutionarily singular strategies are strategies for which the fitness gradient is zero. In the PIP, these points are identified by the intersection of two zero-contours, one of which is the diagonal ($s_{\text{mut}} = s_{\text{res}}$) and the other is not.

Bifurcation diagram

Yet, when the evolving strategy is a scalar and the resident is monomorphic, the evolutionary dynamics can be elucidated also with a bifurcation diagram, e.g., Fig. 2.2. Typically, there is one model parameter on the x -axis and singular strategies on the y -axis. In the bifurcation diagram, the viability region and the type (attracting or repelling) of the viability borders can be shown. Furthermore, the singular strategies are illustrated differently whether they are repelling, attracting, invadable or evolutionarily stable.

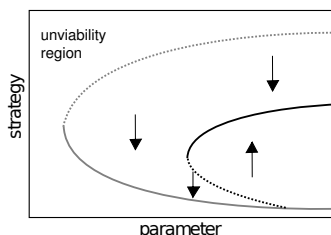


Figure 2.2: A bifurcation diagram showing singular strategies and boundaries of the viability region with respect to a parameter. Attracting ESSs are shown with a black solid curve, repelling strategies with a black dashed curve. Attracting viability boundary is shown with a gray solid curve and repelling viability boundary with a gray dotted curve.

Trait-substitution sequence

A trait-substitution sequence (TSS) is a result of a stochastic process, in which random mutation events and natural selection occur consecutively, e.g., Fig. 2.3. Let the strategy space be denoted by S . Now $\hat{S} = S \cup S^2 \cup S^3 \cup \dots \cup S^n$ defines the space of strategy coalitions up to n coexisting strategies. The TSS $\{S_t \in \hat{S} | t = 0, 1, \dots\}$ is such a sequence of strategy coalitions, in which a strategy coalition S_{t+1} has replaced the strategy coalition S_t . The simplest case involves only monomorphic residents. Then $S_t = \{s_t\}$, where $s_t \in S$. For example, the initial monomorphic resident population has a strategy s_0 . A mutant with a strategy s_1 appears and invades the resident. The strategy s_1 becomes the new, prevalent resident by itself. Then a new mutant with a strategy s_2 does the same, etc. This leads to a trait substitution sequence s_0, s_1, s_2, \dots . In the presence of equal mutational variance and the absence of mutational covariance, the typical mutant s_{t+1} that can replace the resident s_t satisfies

$$s_{t+1} = s_t + \epsilon G(s_t), \quad \epsilon > 0$$

where G corresponds to the fitness gradient, see e.g., Fig. 2.4. Note, that S_{t+1} and S_t may have common elements, but $S_{t+1} \neq S_t$. Note also, that S_{t+1} and S_t may contain different amounts of strategies present.

A trait-substitution sequence may converge to an ESS strategy, s^* (Fig. 2.3a). Strategies may branch and the TSS may converge to a dimorphic evolutionarily stable strategy coalition (Fig. 2.3b). Also, evolutionary suicide may occur (Fig. 2.3c). Theoretically, a periodic TSS is also a possible outcome (not illustrated).

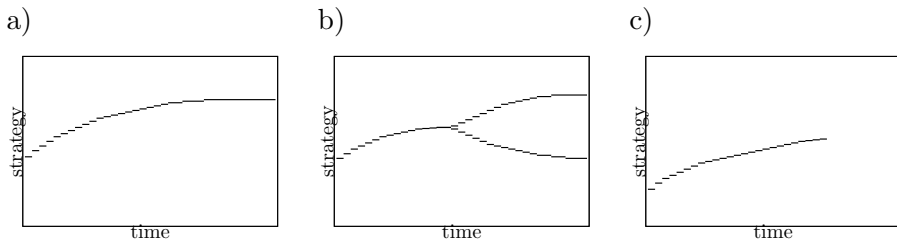


Figure 2.3: Trait substitution sequences may (a) converge to an ESS, (b) result in evolutionary branching or (c) result in evolutionary suicide.

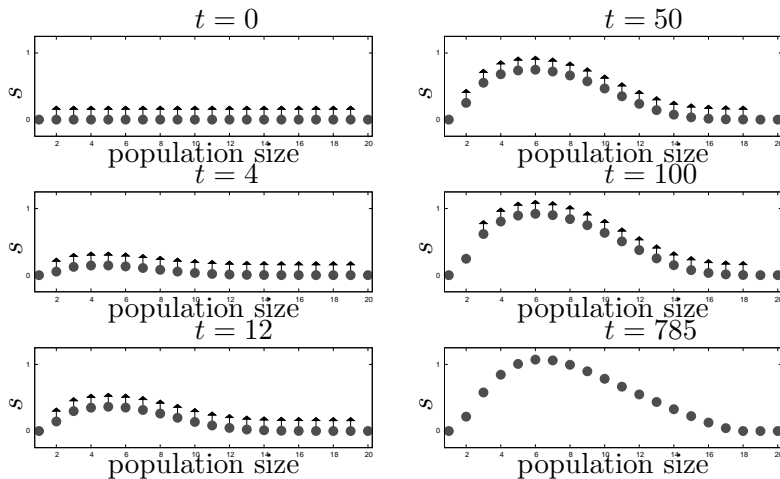


Figure 2.4: A trait substitution sequence, when the evolving strategy is a vector. Each step is taken towards the selection gradient (arrows) and t stands for the simulation steps.

Phase plane plots

When studying more complex strategies, some traditional ways to elucidate evolution become less useful. An example of such complex strategy is

a vector-valued strategy, which can be used when studying joint evolution of two single-valued life history traits, or evolution of a plastic trait like density-dependent dispersal. In such case, by concentrating on two elements in the vector-strategy at the time and having all the other elements fixed or determined by the focal elements, we can illustrate evolution with phase plane plots, in which isoclines of the fitness gradients and evolutionary trajectories are shown, Fig. 2.5.

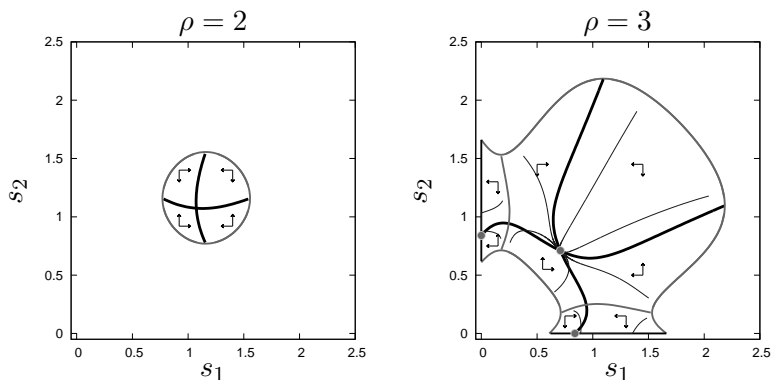


Figure 2.5: Isoclines of the monomorphic fitness gradient together with arrows illustrating the expected direction of evolutionary trajectories. In addition to isoclines, several trait substitution sequences (TSS) are shown in the right hand side panel. Depending on the initial strategy of the monomorphic resident, a TSS will lead to the intersection of the isoclines, or to the boundary of strategy space.

Chapter 3

Main results

In this chapter the main results are reviewed shortly. For details, the corresponding original publications **I-V** can be found attached after the part of General Theory.

3.1 Evolution of dispersal

As mentioned earlier, dispersal, i.e., movement of an individual from a breeding site to another, is a key feature in metapopulations. Dispersal affects patch recolonization and naturally the viability of the whole metapopulation (Levins, 1969, 1970). Therefore, a very intuitive evolutionary question in metapopulations concerns, what selects for or against dispersal.

As with any evolving life history trait, dispersal will be shaped by its costs, benefits and genetic constraints. Dispersal carries energetic and reproductive costs, a disperser is often exposed to, e.g., weather and predator, which make dispersal risky, and hence, selected against (Roff, 1977; Gandon and Michalakis, 2001; Errington, 1946). However, dispersing may also be beneficial. A disperser may immigrate to a habitat with better reproductive success (Metz et al., 1983). Surprisingly, dispersal is favorable even in stable habitats. Hamilton and May (1977) considered an environment with fixed number of sites, each of which can support only one individual. Before its death each adult produces a constant number of offspring. A fraction m will disperse, while the rest will compete at their home site. Only a fraction π of the dispersers survive, and are distributed equally to all the sites. In this simple model, Hamilton and May (1977) showed that evolution of dispersal leads to an evolutionarily stable strategy $m^* = 1/(2 - \pi)$. Dispersal evolves to positive values even with high risk ($\pi \approx 0$). This finding seems rather unintuitive at the first

glance. However, as dispersal allows to avoid competition among kin, the result becomes more obvious. Indeed, dispersal can be understood as an altruistic behaviour.

Unsurprisingly, numerous studies on the evolution of dispersal have been published extending the results of Hamilton and May (1977), e.g., using fully Mendelian approach (Motro, 1982a,b). An interesting question arises from the obvious conflict between the parent and the dispersing offspring: who's decision for emigration is it that is under selection. The fraction of dispersing progeny is larger when the decision is made by the parent compared that when the decision is made by the offspring (Motro, 1983). Frank (1986) put these ideas further, and generalized the modelling approach applying Price's formula for gene frequency changes (Price, 1972). Soon after, Taylor (1988) extended Frank's results with an inclusive fitness model.

In metapopulations, the local dynamics are linked to global dynamics through the movement of individuals. Hence, dispersal influences both, the local and the global dynamics. In return, both of them also contribute to the selection processes that shape the evolution of dispersal. Numerous studies concerning the evolution of dispersal in metapopulations or in structured demes have provided great insight into the factors that select for or against dispersal. Both, inclusive fitness approaches (e.g., Rousset and Ronce, 2004; Jansen and Vitalis, 2007) and invasion fitness approaches (e.g., Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) have been applied. The interpretation of the inclusive fitness is straightforward: it tells whether an event is favorable or not. By using inclusive fitness, one can obtain singular strategies, and distinguish whether they are attracting or repelling. However, one cannot investigate whether an attracting singular strategy is unbeatable or beatable, meaning one cannot claim whether the singular strategy is an evolutionary endpoint or a branching point. Moreover, in complex models, inclusive fitness can be very difficult to calculate, whereas the invasion fitness, or its proxies may be easier to calculate.

Variability between patches is one obvious factor selecting for dispersal. If there is lack of resources in a patch, by dispersing one might find a better place for living. Indeed, in the absence of other mechanisms, sufficient spatiotemporal variation in density (or relatedness) is a necessary condition for dispersal (Balkau and Feldman, 1973; Teague, 1977). Hastings (1983) investigated a metapopulation model defined in continuous time with finitely many patches, and showed that if the population-dynamical attractor is an equilibrium, dispersal is not favoured. The same is true also in corresponding discrete-time metapopulation models (Parvinen, 1999).

The spatiotemporal variation can result, e.g., from cyclic (Doebeli and Ruxton, 1997; Parvinen, 1999) or chaotic (Holt and McPeck, 1996) deterministic local population dynamics, local catastrophes (Gyllenberg et al., 2002; Parvinen et al., 2003; Parvinen, 2006), or locally stochastic population dynamics (Metz and Gyllenberg, 2001; Cadet et al., 2003; Parvinen et al., 2003; Parvinen and Metz, 2008).

Two of the original publications attached here involve the evolution of dispersal. In the original publication **I**, the American pika metapopulation with a scalar-valued dispersal strategy is modelled. The second work, the original publication **II**, is also inspired by pikas, but contains a more generally derived model with small local populations and density-dependent, i.e., vector-valued dispersal strategy.

3.1.1 Evolution of dispersal in American pika metapopulation

American pika (*Ochotona princeps*) inhabits mountainous regions in Northern America. It is adapted to cold temperatures and suffers in heat (Beever et al., 2003). Hence, there have occurred speculations that global climate change (GCC), among other anthropogenic factors, represents a threat to American pikas.

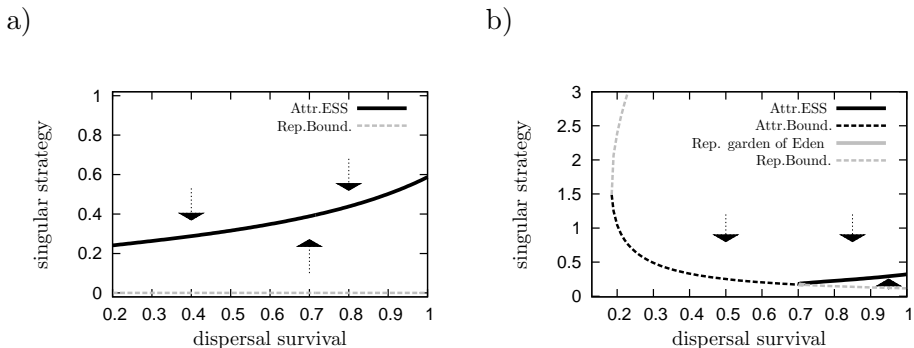


Figure 3.1: Singular dispersal strategies and boundaries of viability with respect to dispersal survival. In the left panel the catastrophe rate is population-size independent, whereas in the right panel the catastrophe rate depends on the local population size. Adopted from Seppänen et al. (2012).

In the original publication **I**, a metapopulation model for studying pikas was derived. The model is semi-discrete, with births and immigration occurring at discrete points in time, and deaths and emigration

occurring continuously over time. To study the possible evolutionary effects of changing climate, global climate change is assumed to potentially alter the model parameters, such as the probability of patch extinction, dispersal costs, mortality and fecundity, e.g., Fig. 3.1.

The results show that potentially viable metapopulations nevertheless can be destined to extinction via evolutionary suicide driven by climatic forcing illustrated in Fig. 3.1b. Specifically, selection can drive down dispersal rates in viable metapopulations, degrading colonization rates and increasing extinction rates to the point where the metapopulation crashes (Seppänen et al., 2012). Also the opposite case is possible. There is a region in the parameter space, where a metapopulation can be very close to its lower viability border and selection for higher dispersal rate can take the dispersal rate away from the extinction boundary.

In this study, evolutionary extinction is shown to be a possible outcome also in a very realistic model setting. As a conclusion it is noted that exclusive reliance on ecological dynamics without this evolutionary perspective would miss the phenomenon identified here. Indeed, evolutionary dynamics should be incorporated into the viability analysis.

3.1.2 Evolution of complex density dependent dispersal in small patch metapopulations

Many life-history traits are density-dependent, i.e., they depend on population size or density. This holds for dispersal too (e.g., Matthysen, 2005). Previous studies of conditional dispersal tend to assume monotone density-dependence in dispersal strategy (e.g., Geritz et al., 2009), or obtain such as a result from theory (e.g., Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). For example, Travis et al. (1999) investigated the evolution of dispersal as a linear function of local population density.

Inclusive fitness can also be used to study the evolution of such life history traits that affect metapopulation demography (Rousset and Ronce, 2004). Jansen and Vitalis (2007) studied the evolution of dispersal in a Levins' type metapopulation setting, and derived a fitness measure, which can be reformulated as inclusive fitness. They assumed fast local population dynamics compared to global (i.e. metapopulation) dynamics, which naturally simplifies the analysis. However, this leads to some contrasting results with other studies, e.g., concerning how catastrophe rate affects dispersal (Gyllenberg et al., 2002). In addition, the modelling approach cannot be generalized to study density-dependent dispersal since all local populations are on their equilibrium.

In metapopulation models with large local populations, density-depen-

dent dispersal is expected to evolve to a single-threshold strategy (Fig. 3.2a), in which individuals stay in patches with local population size smaller than the threshold value and move immediately away from patches with local population size larger than the threshold (Gyllenberg and Metz, 2001). In the original publication **II** the local population size is assumed to be small, and there were no *a priori* assumptions about the particular form that density-dependence can take.

The local dynamics is described with stochastic demographic events, e.g., birth and death, occurring at individual level. Individuals form small groups, which further constitute a structured metapopulation. The absolute maximum for population size in a patch is K . Reproduction is always clonal. Emigration strategy is denoted by $e = (e_1, e_2, \dots, e_K)$ and immigration strategy by $m = (m_0, m_1, \dots, m_{K-1})$. In the case of natal dispersal, $e_n \in [0, 1]$ is the probability that an individual born in a patch with n inhabitants will emigrate immediately after birth. In case of adults, dispersal is not restricted to a once-in-a-lifetime event, so the strategy $e_n \geq 0$ is a rate, a probability to emigrate per time unit, from a patch with n inhabitants. All emigrants enter a dispersal pool. Each disperser encounters patches randomly at rate α , and decides to stay on the patch with the probability $m_n \in [0, 1]$, where n is the local population size in that patch.

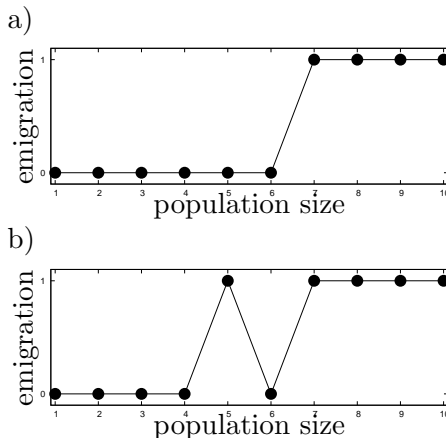


Figure 3.2: Density-dependent dispersal strategy may evolve (a) to a monotone, “single-threshold” state or (b) to a non-monotone, “triple-threshold” state $(0, 0, 0, 0, 1, 0, 1, 1, 1, 1)$.

In this work, it was found that in a metapopulation, where patches can support only a relatively small local population, density-dependent

emigration can evolve also to a non-monotone, “triple-threshold” strategy (Fig. 3.2b). This interesting phenomenon results from an interplay between the direct and indirect benefits of dispersal and the costs of dispersal (Parvinen et al., 2012).

With the parameter values used in Figs. 3.2b and 3.3, the intuitively expected strategy is $(0, 0, 0, 0, 0, 0, 1, 1, 1, 1)$. As illustrated with phase-plane plots in Fig. 3.3, isoclines of the selection gradient and thus, also singular strategies depend on the catastrophe rate μ . Now, the point $e_5 = 0$ and $e_6 = 0$ (the lower left corner) in Fig. 3.3 corresponds to the strategy shown in Fig. 3.2a and the point $e_5 = 1$ and $e_6 = 0$ (the lower right corner) in Fig. 3.3 corresponds to the strategy shown in Fig. 3.2b. In specific, the isoclines and trajectories illustrate that the latter (“triple-threshold”) strategy is evolutionarily attracting in panels b-f. Note that in the TSS calculations all strategy components are freely evolving.

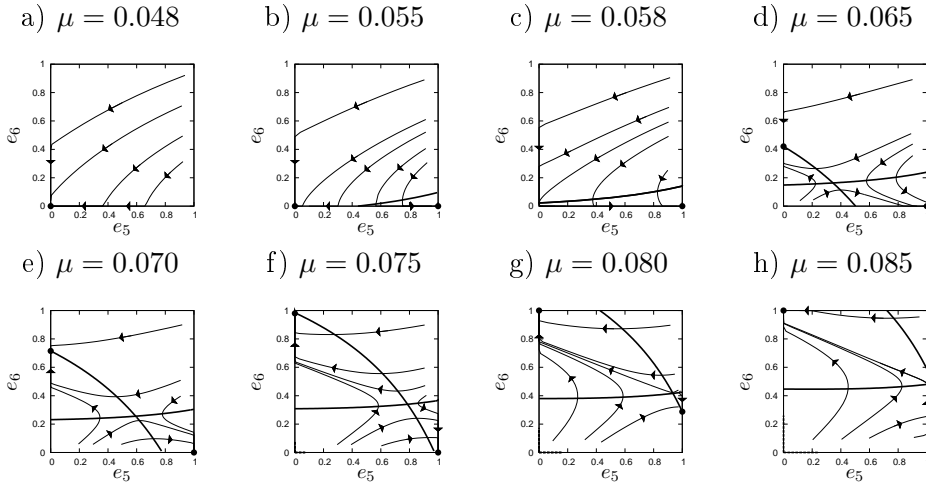


Figure 3.3: Phase plane plots for the strategy components e_5 and e_6 , while other components are constant ($e_1 = e_2 = e_3 = e_4 = 0$ and $e_7 = e_8 = e_9 = e_{10} = 1$). Direction of the selection gradient and singular strategies (black dots) alter along the catastrophe rate μ changes. Some sample trajectories of TSS calculations are also elucidated. Adopted from Parvinen et al. (2012).

In the original publication **II**, the evolution of density-dependent dispersal to a non-monotone shape was explained as an interplay between direct and indirect fitness benefits and fitness costs, comparable to inclusive fitness. The fitness calculations were based on the metapopulation reproduction ratio. As noted before, the fitness measure includes both,

the direct and the indirect fitness benefits, but is so complicated that it is hard to divide into the corresponding parts. To achieve some insight, the metapopulation reproduction ratio was divided into parts E_k according to the local population size. The measure E_k is the expected production of mutant dispersers for a mutant clan initiated by a mutant immigrant arriving to a patch with $k - 1$ residents. As the invasion fitness, the measure for E_k also includes both direct and indirect benefits, which again are difficult to disentangle. A quantity consisting of E_k and relatedness describing the benefit of dispersal was investigated, see Fig. 3.4. Detailed explanation is in the appendix of the original publication **II**. However, this does not fully explain the observed phenomenon. The actual fitness gradient shows correctly that the single-threshold strategy is repelling, but since the measure is difficult to separate into direct and indirect components it does not provide intuition in an easy manner.

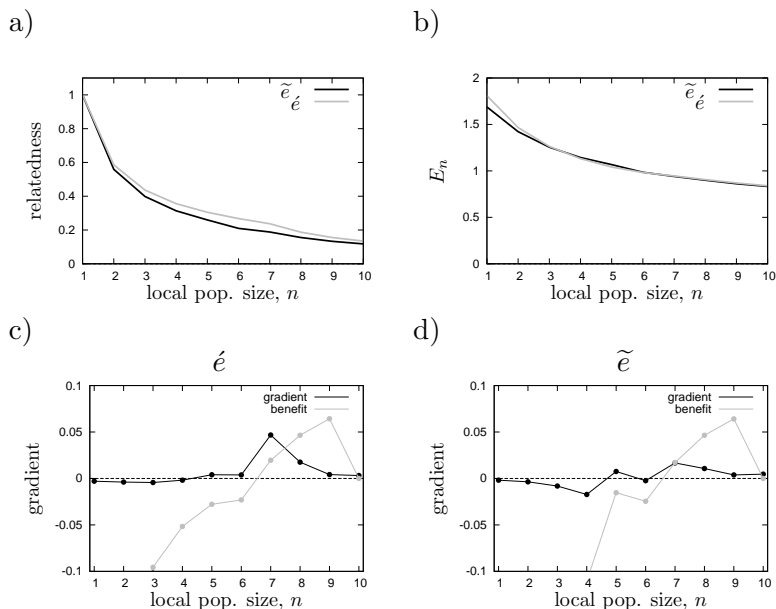


Figure 3.4: Illustration of the intuitive threshold strategy $\acute{e} = (0, 0, 0, 0, 0, 0, 1, 1, 1, 1)$ and the multiple threshold strategy $\tilde{e} = (0, 0, 0, 0, 1, 0, 1, 1, 1, 1)$: (a) relatedness, (b) decomposition E_n of invasion fitness at metapopulation-dynamical equilibrium. (c and d) Approximate benefit of emigration and the fitness gradient. Adopted from Parvinen et al. (2012).

This study uncovers a very surprising phenomenon concerning density-dependent natal-dispersal. Evolutionarily attracting and stable non-mono-

tone, multiple threshold strategies, were found. Although this type of non-monotone strategy might be hard to detect in natural systems, the contribution was to show a very unintuitive evolutionary phenomenon. The general conclusion from this work is that one should be cautious when building models on an assumption of monotone density dependence, especially in models dealing with dispersal.

3.2 Evolution of cooperation

Plato, a great philosopher in Classical Greece, presented his ideas of justice and ideal social structures in his most famous dialogue, *The Republic*, already about 380 BC. Later, Hardin (1968) described a related problem in 'The tragedy of the commons'. Ever since, the phenomena of altruism, cooperation and defecting behaviour have puzzled and inspired researchers from diverse disciplines.

Huge interest in the issue has yielded to a broad theoretical framework based on game theory (Axelrod and Hamilton, 1981; Sigmund et al., 2001; Nowak and Sigmund, 2005). For example, in the Prisoner's dilemma game, two individuals have committed a crime. In an interrogation, both have the option to pleading guilty or not guilty. If both confess the crime, they get two years sentence. If both deny, they get only one year in prison. If one admits, while other one denies, the defector will be set free and the honest one gets three years.

	C	D
C	R(-1)	S(-3)
D	T(0)	P(-2)

This game is obviously context independent. In more abstract description we say, individuals are of two types, cooperators and defectors. When two cooperators meet, they are rewarded with a payoff R , and when two defectors meet they are punished and the payoff is P . In an interaction of unequal types, the payoff for the cooperator is S (sucker) and for the defector T (temptation). It is also assumed that $T > R > P > S$. For an independent individual the best strategy is to defect. However, the dilemma arises as the payoff for mutual cooperation would yield better outcome.

Another famous game is the Hawk-Dove game. The setting is similar to the Prisoner's dilemma game. There are two possible strategies, hawk and dove, referring to aggressive behavior of the subtype. There is resource available, and the individuals may fight for it. Aggression is costly, and C represents the cost or damage from loosing in a fight. Hawks always fight

for the resource, and doves don't. When two doves meet they share the resource in peace. This gives a payoff matrix:

	Hawk	Dove
Hawk	$B/2 - C/2$	B
Dove	0	$B/2$

The above games occur in pairwise interactions. However, many cooperative actions take place in bigger groups of individuals. Then public-goods games are applicable. In a public-goods game each player can invest independently to a common resource, which typically is multiplied with a gain factor. In the end, all players get an equal share of the common good. Again, a defector, who does not contribute, but receives a benefit from other's contribution, obviously has the greatest pay-off.

Cooperation is highly common in life, even though it is vulnerable for defecting. This observation has puzzled researchers from many fields, and indeed, there exist factors that select for cooperative behavior (Nowak, 2006), like kin benefits (Hamilton, 1964a,b) and reciprocity (Trivers, 1971). If same individuals meet repeatedly, and are able to remember some past actions, direct reciprocity may lead to cooperation. For example, Axelrod and Hamilton (1981) showed that tit-for-tat, that is imitate the strategy of the opponent from the last round, is an evolutionary stable strategy in a repeated prisoner's dilemma game. Reciprocity can also be indirect, when population follows some social norms. Some individuals do not necessarily meet twice, but they may build good reputation by cooperating. The evolution of cooperative behaviour may lead to complex social structures with ever-increasing cognitive demands (Sigmund et al., 2001; Nowak and Sigmund, 2005)

In general, cooperation can arise and be maintained when cooperators are sufficiently likely to interact with cooperators (Sherratt and Roberts, 2012). This means that there can be various mechanisms behind the assortment, such as kin selection or spatial factors. Eventually it is the level of assortment, not so much the mechanism behind the assortment, what actually matters. Furthermore, the evolution of cooperation is involved in all the major transitions in evolution (Maynard Smith and Szathmáry, 1995), e.g., the origin of multicellularity and the emergence of societies.

Two of the original publications, **IV** and **V**, indeed, concern the evolution of cooperation. The original publication **IV** studies the evolution of density-dependent cooperation in a metapopulation with small local populations. Finally, the publication **V** investigates the evolution of cooperative investing in a public-goods game with two resources. There evolution

leading to two coexisting subpopulations specialized in the production of different resources is interpreted as labour division.

3.2.1 Evolution of density-dependent cooperation

In previous models, public goods cooperation has been assumed to be either an on-off strategy (e.g., Hauert et al., 2006) or a quantitative but condition-independent strategy (e.g., Parvinen, 2010, 2011). Nevertheless, it is rather realistic to assume that individuals, higher as well as lower organisms, are capable to sense the population density in their neighborhood, and to adjust their investment to common resources based on that information (Pai et al., 2012). The focus in the original publication **IV** is on plastic, quantitative cooperation behaviour, and especially on its evolution.

The ecological setting is described with stochastic demographic events, e.g., birth and death, occurring at individual level. Individuals form small groups, which further constitute a structured metapopulation. Intuitively, one would expect plastic cooperative investments to be highest in small groups and always to decrease when the local population size increases. This intuition arises from the expectation that relatedness decreases as the group size becomes bigger. Similar to the original publication **II**, the metapopulation reproduction ratio includes both direct and indirect fitness benefits, which are extremely difficult to disentangle.

The cost of cooperative investment was incorporated into the model in two different ways, either it decreases the birth rate or increases the death rate of the cooperator. In the first case, density-dependent cooperation evolves to be a decreasing function of group size as intuitively expected. In the latter case, however, the density-dependent cooperative investment can have a qualitatively different form as it may evolve to be highest in intermediate-sized groups (Fig. 3.5b). Contradicting the *a priori* intuition, this hump-shaped cooperation is to some extent surprising.

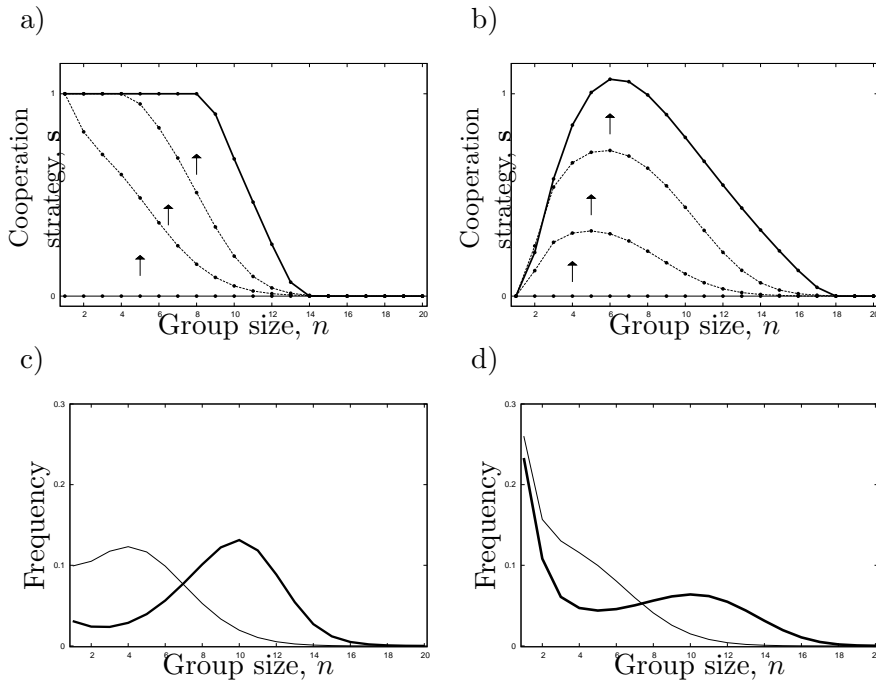


Figure 3.5: The emergence of plastic cooperation and its effect on the group size distribution, when the cost of cooperation is modelled through decreasing the birth rate (left column, a,c) or through increasing death rate (right column, b,d). (a,b) Evolutionary dynamics of density-dependent cooperation initiated with a total defector strategy ($s = 0$, thin solid line) resulting in an evolutionary stable strategy (ESS, bold line). (c,d) Proportions of different group sizes for the total defector (thin solid line) and the ESS cooperator (bold line) in their ecological equilibrium. Compared with the defector groups, the cooperating groups reach on average higher sizes.

The novelty in this study is to consider cooperative investment to be density-dependent, which is indeed a realistic assumption. Already simple cells are able to coordinate their behaviour as a response to population density through a mechanism called quorum sensing. This would include regulation of gene expression levels and secretion of factors considered as common good (Miller and Bassler, 2001; Diggle et al., 2007). An interesting finding was that the form of the evolutionary stable strategy can be qualitatively different depending on the way how the cost of cooperation is modelled (compare Fig. 3.5a and 3.5b). Some heuristic explanation for this difference is also provided in the original publication **IV**. Indeed, it is emphasized that some details in modelling may have a significant impact

on the results obtained. In addition, as expected, cooperative groups were able to grow not only bigger than defector aggregates but also well beyond the carrying capacity (Fig. 3.5b).

3.2.2 Evolution of labour division

Labour division among cooperating entities is a common pattern in living systems and an important requisite for the development of complexity. Increasing division of labor is widely thought to be a hallmark of modern human culture, economics and industrialization (Cassata and Marchionatti, 2011; Ghiselin, 1995; Kuhn and Stiner, 2006). In economics, it is well known that "the division of labour is limited by the extent of the market" (Smith, 1776; Stigler, 1951). To translate this result in a biological context, the organism size serves as an analogy for the market size, and indeed, it must reach a certain size before tissue differentiation is observed (Bonner, 2003).

(Rueffler et al., 2012) identified three general factors selecting for division of labor; positional effects, accelerating performance, and synergistic interactions. Also task switching might be costly and hence, select for division in labour (Goldsby et al., 2010, 2012). Furthermore, plastic development (Gavrilets, 2010) can lead to the emergence of labour division.

The aim in the original publication **V** was to elucidate the emergence of labour division in a simple probabilistic model with public-goods game. The model was first described in its simple form by Hauert et al. (2006) and later generalized by Parvinen (2010). In this study, the model was generalized further assuming that there are two common resources. In order to have functional specialization possible, two common resources are needed. Individuals play in small randomly gathered groups. In a game, individuals can invest on two common resources depending on their phenotype. Resources are then shared among the players in the group. Consumption of the two resources, when they are available, is beneficial in reproduction. Thus, investments on cooperative act can be paid off.

In this study it is shown that evolutionary branching can generate cooperative division of labor among subpopulations specializing in the production of only one of the two resources (Fig. 3.6a). Also, other evolutionary outcomes are possible: a strategy coalition with a generalist cooperator and a defector (Fig. 3.6b), or a monomorphic population with only a specialist cooperator (Fig. 3.6c). In addition, altering model parameters result in several evolutionary bifurcations generating potentially rich evolutionary dynamics.

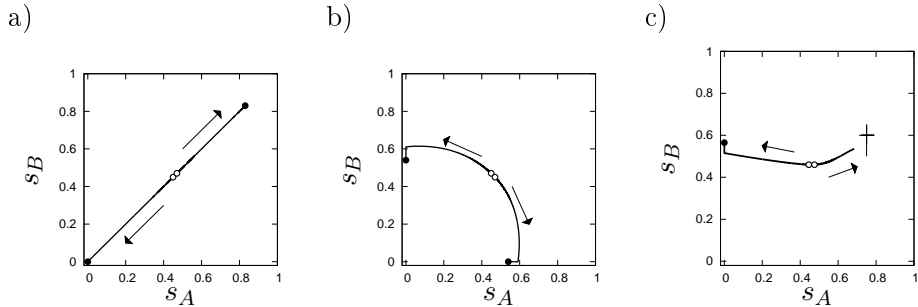


Figure 3.6: Trait substitution sequences initiated with different dimorphic strategy coalitions near the monomorphic attracting singular strategy, which is invadable. Dimorphic evolution may lead (a) to the coexistence of a defector and a generalist cooperator, (b) to the coexistence of two specialist producers (labour division), or (c) to one specialist producer only.

3.3 Methodological derivations

The inspiration for the studies here have arisen from natural populations and related evolutionary questions. Nevertheless, it was necessary to improve the methods and theory to be able to implement the applications and study the evolutionary problems. Within this thesis project two novel methods have been derived, both of which are derivations of the metapopulation reproduction number as a proxy for the invasion fitness.

3.3.1 Invasion fitness in a semi-discrete-time metapopulation

In the original publication **I**, a metapopulation model in semi-discrete time is introduced. However, there was no proxy available to calculate the invasion fitness in that model. Thus, a proxy for invasion fitness in a metapopulation with semi-discrete population dynamics was necessary to derive. The idea is to calculate the expected number of dispersers produced by a mutant clan initiated with a single mutant. First, the probability that a mutant immigrant survives until next phase change, is calculated. From there on, for all mutant clans, it is a book-keeping task to calculate how many dispersers they send in each year and also how the whole clan survives through the seasonal phases.

In our model, pikas experience a sequence of “phases” or seasons throughout the year in which population-dynamic forces vary. Each year,

population census occurs at time $t = 0$, weaning of the young occurs at time τ_1 , after which the juvenile may emigrate until $t = \tau_2$. During the early summer season ($\tau_1 < t < \tau_2$), all individuals suffer from mortality. In addition, juveniles on patches both search for empty territories and challenge adults and other juveniles for territories. All dispersers enter a global dispersal pool and are randomly distributed among patches at a discrete point in time, τ_2 . After immigration, i.e., during the late summer season ($\tau_2 < t < 1$), local (within-patch) dynamics continue as before but without emigration. The patch into which an immigrant arrives has age ξ with probability $p(\xi)$. Let $P_{D \rightarrow 1}(\xi)$ denote the probability that a mutant immigrant to a patch of age ξ successfully survives until the census. In the pika-model, it was necessary that the immigrant also settles to a territory to be counted at census. The values of $P_{D \rightarrow 1}(\xi)$ are solved from a system of differential equations. A local population in a patch goes extinct over winter with probability $\mu_c(A(\xi))$, where $A(\xi)$ is the local adult population size at census. Then, the mutant survives to the following year with probability $1 - \mu_c(A(\xi))$. This mutant will be the ancestor of a mutant lineage (also called a mutant clan) in this patch, currently of age $\xi + 1$.

Let $E(\xi + 1)$ denote the cumulative number of emigrated mutant juveniles over all coming years in the lineage established by a single mutant ancestor. Using this notation the metapopulation reproduction ratio

$$R_{\text{mut}} = \sum_{\xi=0}^{\infty} p(\xi) P_{D \rightarrow 1}(\xi) (1 - \mu_c(A(\xi))) E(\xi + 1), \quad (3.1)$$

is obtained. It is the expected number of all future dispersing descendants of a mutant immigrant, in an environment set by a resident in a metapopulation-dynamical equilibrium. To obtain $E(\xi + 1)$, a recursion can be derived. That is explained in detail in the original publication I (Seppänen et al., 2012).

3.3.2 Invasion fitness in a size- and stage-structured metapopulation

When a size-structured metapopulation model involves also individual stages, e.g., juvenile and adult stages resulting from maturing or development, there exists a generalized definition for the invasion fitness. The idea is to calculate the expected numbers of dispersers of all different possible types produced by a mutant clan initiated with a single mutant, and to collect these values into a matrix. The matrix describes the production of the next dispersing generation, and its elements (i, j) stand for the production of dispersing type j when the clan was initiated by an immigrant

of type i . The metapopulation reproduction ratio is then the dominant eigenvalue of this matrix. The calculation method was published in detail in the case of small local populations (Parvinen and Metz, 2008). However, for a metapopulation with infinite local populations, there has been no generalized method available.

In the original publication **III**, a generalized method to calculate the invasion fitness in a metapopulation, which consists of large local populations with dynamics described in continuous time, when the metapopulation is both size and stage structured, is derived (Parvinen and Seppänen, subm).

In this work, it is proved that the metapopulation reproduction ratio is well-defined, i.e., it is equal to 1 for a mutant with a strategy equal to the strategy of a resident. For this class of models, such a proof has not been previously published even for the case with only one type of individuals.

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