

ADAPTIVE DYNAMICS  
IN FLUCTUATING ENVIRONMENTS  
AND ITS APPLICATION IN EVOLUTIONARY STUDIES

YUHUA CAI

ACADEMIC DISSERTATION

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April 20, 2021, Helsinki  
Yuhua Cai



## Abstract

This article-based dissertation aims to understand by means of mathematical models how organisms evolutionarily respond to fluctuations in the environment. It uses the approach of adaptive dynamics to study the long-term evolution of phenotypic strategies in an environment that fluctuates in time because of biotic interactions and/or external factors. The dissertation demonstrates how this approach can reveal clear-cut explanations for complex environment-phenotype relationships by one general method-oriented article and two case studies in two additional articles.

In the first article, I show that under the standard assumptions of adaptive dynamics, in particular mutation-limited evolution and small mutation steps, the generic dynamics of the resident-invader population in fluctuating environments can be fully characterized in terms of the behaviour near the boundaries of population state space, which in turn can be determined by the invasion criteria. This generalizes previous results for unstructured populations in a constant environment, which is important because it justifies the use and interpretation of various methods in the theory of adaptive dynamics for a significantly larger class of ecological situations that include fluctuating environments and structured populations.

The two case studies are applications of the classification of invasion outcomes to explore the long-term evolutionary consequences of many successive invasion events. In the first case study, I investigate the evolution of the irreversible transition from a free-swimming state to an immobile sessile state as seen in many aquatic invertebrates. To this end, I study the adaptive dynamics of the settling rate of a hypothetical microorganism onto the wall of a chemostat with a fluctuating nutrient availability. The results show that different dilution rates and spatial competition mechanisms, as well as different frequencies of the nutrient fluctuations, have qualitatively different effects on the evolution of the settling rate as well as on species diversity. The model generates several hypotheses for further empirical studies.

In the second case study, I investigate the evolution of the colonization rate in an extended competition-colonization model with ownership effects and stochastically varying mortality rate. I find that the strength of the trade-off, ownership effect and fluctuation intensity all have a non-monotonic effect on the emergence of species diversity via evolutionary branching. In particular, intermediate disturbance—as measured by the fluctuation intensity of the mortality rate—promotes evolutionary branching and hence the emergence of polymorphisms.

This provides new evidence for the intermediate disturbance hypothesis. I also find that there can be multiple evolutionary attractors for polymorphic populations, each with its own basin of attraction. Consequently, random mutation-induced transition of coevolutionary trajectories between neighbouring basins of attraction makes the long-term evolutionary outcome uncertain.

By means of these examples, the dissertation demonstrates that the approach of adaptive dynamics is a powerful tool for untangling the connection between environmental changes and adaptive strategies.

## List of original articles

This dissertation consists of an introductory part and the following three scientific articles:

- I Cai, Y., Geritz, S.A.H., 2020. Resident-invader dynamics of similar strategies in fluctuating environments. *Journal of Mathematical Biology* 81: 907–959. doi:10.1007/s00285-020-01532-8
- II Cai, Y., Geritz, S.A.H., 2021. The evolution of the irreversible transition from a free-swimming state to an immobile sessile state in aquatic invertebrates modelled in a chemostat. *Journal of Theoretical Biology*, 522: 110681. doi:10.1016/j.jtbi.2021.110681
- III Cai, Y., 2021. Long-term coexistence in a metacommunity: competition-colonization trade-off, ownership effects, environmental fluctuations. Under review.

## Author's contribution

I had the leading role in the research carried out for all of the three articles as well as in the writing of manuscripts. I am the corresponding author in Articles I and II and the sole author in Article III.





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# Chapter 1

## Introduction

Organisms exhibit diverse phenotypic strategies for adapting to fluctuating environments (Kussell and Leibler 2005). Individual strategies can be (*i*) morphological (outward appearance such as shape, structure or size as well as internal form such as bones and organs), (*ii*) physiological (body chemistry such as digestion and hormonal regulation) or (*iii*) behavioural (specified by individual states and state transitions). The environment of an individual is everything that affects its behaviour. This usually includes abiotic factors such as the weather but also all individuals with which it interacts. The origin of environmental fluctuations thus may be purely demographic (i.e., stochastic fluctuations due to small population size, or cycles or chaos due to population interactions), or they may be the result of stochastically varying factors of the physical environment (e.g., temperature, humidity or pollution) (Lande et al. 2003). The dissertation considers fluctuations due to population interactions and fluctuations in the physical environment, but it does not consider fluctuations due to small population size.

In a stochastically and hence unpredictably varying environment, individuals can reduce the impact of unfavourable conditions for instance by spreading germination in time using a soil seed bank (Cohen 1966; Venable 2007), spreading reproduction in time as opposed to a single reproductive burst (Cunnington and Brooks 1996; Janzen et al. 2000), or spreading out breeding efforts in space and time by long-distance migrations (Holland et al. 2006; Dingle 2014). This way of coping is called the bet hedging principle (see, e.g., Seger and Brockmann 1987; Philippi and Seger 1989; Olofsson et al. 2009; Simons 2011; Mayer et al. 2017; Xue et al. 2019).

In periodic and hence predictable environments, different principles may apply such as conditional differentiation (also called temporal niche separation) where a strategy specializes on a particular phase of the environmental cycle. For instance, some desert plants are more successful during wet years while others are more successful during dry years (Angert et al. 2009), or being active during the good times while being inactive during the bad times such as day-night cycle in the desert and summer-winter cycle in the (sub-)arctic (Holzapfel 2008; Hairston and Fox 2013). Conditional differentiation promotes coexistence of different strategies specializing on different parts of the environmental cycle.

The general aim of the dissertation is to understand how organisms evolutionarily respond to fluctuating environments (stochastic or otherwise) in terms of general principles and using mathematical models.

Evolution is the ongoing change in heritable strategies of the individuals of a biological population over successive generations due to natural selection and random mutation. Natural selection is just population dynamics, namely, the elimination of individuals whose strategies that make them less competitive or more vulnerable to predation or disease than others. Random mutation is the process of the generation of new heritable strategies through alterations in the genome. Natural selection and random mutation are antagonistic processes in the sense that one reduces variation while the other increases variation. The main questions of evolutionary studies are how these two processes shape the long-term strategy dynamics and how it connects to genetic and ecological principles.

There are various modelling approaches to study evolutionary processes, each with its own focus, merits and limitations. For instance, *(i) Population Genetics* studies the dynamics of allele frequencies and genotypes using models with explicit genetics (Crow and Kimura 1970). In this way, we gain evolutionary insight in terms of fundamental genetic principles. However, the genetic complexity of the models practically excludes the implementation of complicated ecological interactions. *(ii) Evolutionary Game Theory* uses the theory of games to study the evolutionary consequences of the costs and benefits of different strategies (Maynard Smith 1982). In particular, it has much improved our insight into the evolution of animal behaviour in situations of conflict of interest. A notable limitation is its focus on evolutionary equilibria (i.e., evolutionary stable strategies) and hence a disregard of evolutionary dynamics. *(iii) Adaptive Dynamics* studies the gradual evolution of phenotypic strategies in potentially complicated ecological systems, and explicitly links long-term evolution to population dynamics (Metz et al. 1992; Dieckmann and Law 1996; Metz

et al. 1996; Geritz et al. 1997, 1998, 1999). Adaptive dynamics has given us an understanding of various kinds of dynamical evolutionary phenomena such as evolutionary branching, evolutionary cycles and extinction.

The dissertation focuses on adaptive dynamics. While the above is not an exhaustive list of approaches, it puts adaptive dynamics in a wider context. I mention evolutionary game theory, because adaptive dynamics can be seen as its extension by including evolutionary dynamics. I mention also population genetics, because it is almost the complement of adaptive dynamics: it considers full genetic detail but almost completely ignores ecology, while adaptive dynamics has ecology at its core but typically uses only the most basic genetic mechanism, namely, clonal inheritance.

The dissertation contributes with new general results and gives comprehensive applications to two specific ecological-evolutionary problems. Adaptive dynamics is a relatively new approach and is being used in a rapidly increasing number of studies of ecological-evolutionary problems. However, there does not yet exist a well-developed theory of adaptive dynamics for stochastically varying populations and stochastic environments. Stochastic fluctuations are common in nature and can have a significant effect on the ecological and evolutionary dynamics of populations. For instance, fluctuation can promote coexistence but also can cause extinction (Chesson and Warner 1981; Chesson 1986; Tuljapurkar 1990; Holt et al. 1994; Benaïm and Lobry 2016; Hening and Nguyen 2020), fluctuation crucially influences evolutionary fitness functions (Melbinger and Vergassola 2015), and fluctuation often increases the dimension of the ecological feedback environment (see Fig. 1) so that more species can coexist (Kisdi and Geritz 2016). Consequently, it is important and necessary to extend the approach of adaptive dynamics to take these fluctuations explicitly into account.

The dissertation consists of an introductory part and three scientific articles. The first part provides a clear overview of the research content with minimal emphasis on technicalities. The rest of this part is organized as follows. Chapter 2 presents the research questions, methods and results. Chapter 3 describes how to make a stochastic population model. Chapter 4 briefly presents the approach of adaptive dynamics used in the scientific articles. The second part, composed of the scientific articles, serves as the main body of the dissertation.



## Chapter 2

# Questions, methods and summary

This chapter focusses on the research questions, the methods that have used to address them, the main results obtained, and the new questions raised by the research.

### 2.1 Research questions

Three of the central problems are addressed in the dissertation:

- Q1:** how do the strategies of the individuals that make up a population affect the long-term population dynamics in a fluctuating environment?
- Q2:** what kind of mutants can invade (i.e., increase in population density) and what will be the population dynamical consequences of such an invasion event in terms of which strategies will survive and which will go extinct?
- Q3:** what will be the long-term evolutionary consequences of many successive invasion events in terms of changes in the strategy composition and the dynamical behaviour of the population?

These questions are closely related, and the answer to each provides support for solving the next question.

## 2.2 Models

Throughout the dissertation, I consider ecological systems that can be described by the following system of equations.

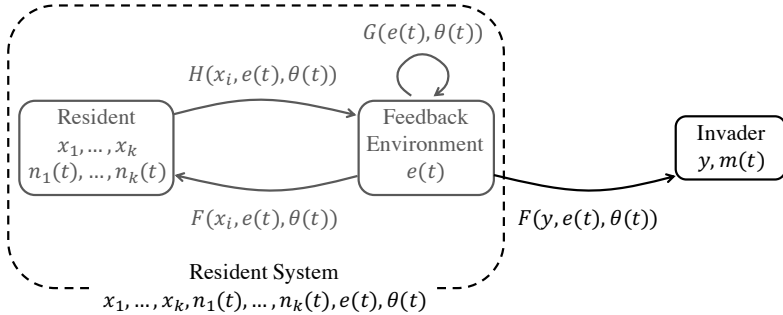
$$\begin{aligned}
 \frac{dn_i(t)}{dt} &= F(x_i, e(t), \theta(t))n_i(t), \quad i = 1, \dots, k, \\
 \frac{de_1(t)}{dt} &= G_1(e(t), \theta(t)) + \sum_j H_1(x_j, e(t), \theta(t))n_j(t), \\
 e_2(t) &= G_2(e(t), \theta(t)) + \sum_j H_2(x_j, e(t), \theta(t))n_j(t), \\
 \frac{d\theta(t)}{dt} &= A(\theta(t)) + B(\theta(t))\frac{dW(t)}{dt}.
 \end{aligned} \tag{2.1a}$$

In (2.1a), population densities  $n_1(t), \dots, n_k(t)$  are elements of  $\mathbb{R}_+^\ell$  for all  $t \geq 0$ , where for  $\ell \geq 2$  we have structured population. Strategies  $x_1, \dots, x_k$  are elements of  $\mathbb{R}^d$  with  $d \geq 1$ . The environment  $(e(t), \theta(t))$  splits into two parts: the part that both affects and is affected by the population densities is called the ecological feedback environment and is denoted by  $e(t) \in \mathcal{E}$ , the part that is not affected by anything but that may affect the population densities as well as the feedback environment is called the driver of the system and is denoted by  $\theta(t) \in \Theta$ , where  $\mathcal{E}$  and  $\Theta$  are assumed to be subsets of normed vector spaces. The feedback environment  $e(t)$  can include the population itself, other interacting populations, and certain physical factors that both affect and are affected by the population such as soil humidity.  $e_1(t)$  and  $e_2(t)$  describe different kinds of feedback variables that some are given implicitly (by differential equations) and others may give explicitly, which make up  $e(t)$  and have been demonstrated in many specific models (e.g., Examples 1 and 2 shown in Article I).

Functions  $F$ ,  $H_1$  and  $H_2$  describe the feedback between the environment and the population living in (Fig. 1), where the impact of the environment  $(e(t), \theta(t))$  in the growth of the population of strategy  $x_i$  is characterized by  $F(x_i, e(t), \theta(t))$ , and where the impact of an individual with strategy  $x_j$  in the environment  $(e(t), \theta(t))$  is characterized by  $H_1(x_j, e(t), \theta(t))$  and  $H_2(x_j, e(t), \theta(t))$ . The dynamics of virgin environment (i.e., the environment unaffected by the population of  $x_1, \dots, x_k$ ) are characterized by functions  $G_1(e(t), \theta(t))$  and  $G_2(e(t), \theta(t))$ . To describe the dynamics of  $\theta(t)$ , the stochastic differential equation used here is not unique, other possible types can be found in Section 3.2.

Once researchers have a specific stochastic population model, they can immediately rewrite it into the generic form (2.1a), which also is demonstrated in





**Fig. 1** Interaction between the resident and the feedback environment and the one-directional impact on the invader, as illustrated by the author and used in Article I.

Article I. How does one make a stochastic population model? Chapter 3 will illustrate the modelling approach for a population consisting of individuals with given strategies and behaviours in a fluctuating environment.

(2.1a) defines a resident system that is assumed to be reached its dynamical attractor (e.g., equilibrium state, periodic orbit or invariant probability measure) so that the population is non-growing and stochastically persistent. The non-growing means the long-term zero growth. Stochastic persistence is defined in the sense that the probability of a population being near extinction is arbitrarily small (Schreiber et al. 2011; Benaïm 2018, see also the detailed explanation in Article I).

When an initially rare mutant  $m(t)$  with strategy  $y$  arrives, the population dynamics of the mutant are given by

$$\frac{dm(t)}{dt} = F(y, e(t), \theta(t))m(t). \quad (2.1b)$$

Fig. 1 illustrates the relationship of the resident system and the invader, where the resident system determines the ecological environment of the invader and hence affects the dynamics of invader, but the initial size of invader is too rare to have negligible impact on the resident.

(2.1) is a generic form of models describing the dynamics of resident-invader population in fluctuating environments, which is intuitive and interpretable in biology and covers a large class of ecological communities in reality.

## 2.3 Methods and main results

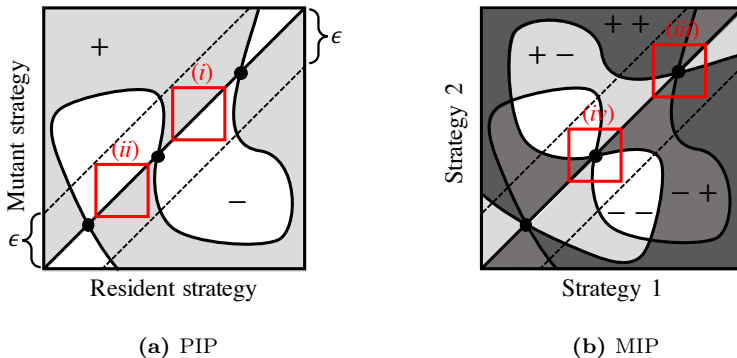
Article I solves questions **Q1** and **Q2** for the general system (2.1). Articles II and III apply the results of Article I to answer question **Q3** for two more specific examples. Next, I will elaborate on how they contribute to addressing these research questions.

Article I considers the resident-invader dynamics in fluctuating environments when the invader and the resident have close but distinct strategies. The article provides a complete classification of generic population dynamical outcomes of an invasion event when the resident population in a given environment is non-growing on the long-run and stochastically persistent. Central to the approach is the series expansion of the model (2.1) with respect to the small strategy difference and the analysis of a stochastic fast-slow system induced by time-scale separation. The article shows that the resident-invader dynamics develops inside a “tube” where the total size of the resident and invader population varies fastly and is arbitrarily close to the former resident attractor (see also Geritz et al. (2002) for the Tube theorem of adaptive dynamics), while the relative size of the invader population as a fraction of the total population size changes slowly (for the case of structured population, a proxy of the relative size are needed in order to construct a purely stochastic fast-slow system, refer to the supplementary material for details). Therefore, the classification of generic population dynamical outcomes of an invasion event is based on the asymptotic behaviour of the relative population size.

If the difference between the strategies of the resident and the mutant goes to zero, then the slow dynamics of the relative population sizes becomes deterministic and one dimensional in spite of population structure and environmental fluctuations.

If the difference between the strategies of the resident and the mutant is positive but sufficiently small and is denoted by  $\epsilon$ , then there are only four different generic possibilities for the slow dynamics of their relative population sizes.

- (i) If the mutant can invade a population of the resident, while under reversion of roles the resident cannot invade a population of the mutant (e.g., strategy pairs in the light grey area of the  $i$ -block in Fig. 2a), then there is no interior attractor, and the mutant will expel the resident and become the new resident itself (Fig. 3*i*).
- (ii) In the opposite situation, i.e., if the mutant cannot invade the resident, while the resident can invade a population of the mutant (e.g., strategy



**Fig. 2** Examples of Pairwise Invasibility Plot (PIP) and Mutual Invasibility Plot (MIP) for illustrating the generic invasion outcomes (i), (ii), (iii) and (iv), where “+” and “-” are signs of the invasion fitness for given strategy pairs and “•” marks the singularity.

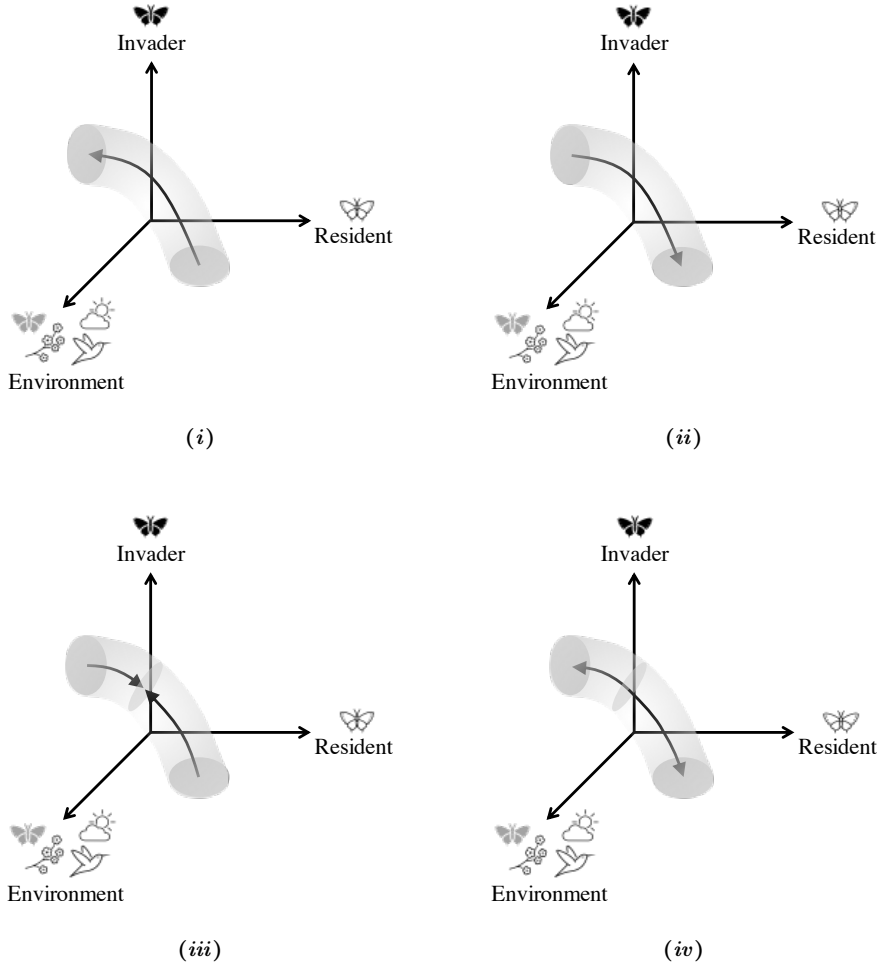
pairs in the empty area of the *ii*-block in Fig. 2a), then again there is no interior attractor, but since the mutant cannot invade, the resident population stays the same (Fig. 3ii).

- (iii) If the mutant and the resident can each invade a population of the other (e.g., strategy pairs in the dark grey area of the *iii*-block in Fig. 2b), then they will coexist at a unique and interior attractor, and the population thus changes from being monomorphic to dimorphic as the former resident and mutant both become the new residents (Fig. 3iii).
- (iv) If neither the mutant nor the resident can invade a population of the other (e.g., strategy pairs in the empty area of the *iv*-block in Fig. 2b), then there exists a separatrix in the interior separating the basins of attraction of the two boundary attractors, but as the mutant cannot invade, the resident population stays the same (Fig. 3iv).

These are the only four generic outcomes of the resident invader dynamics for small strategy differences. Multiple attractors can occur, but only under special additional conditions. Moreover, cases (iii) and (iv) generically\* only happen in a small neighbourhood of a singular strategy (i.e., where the selection gradient vanishes). Geritz (2005) and Dercole and Geritz (2016) found the

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\*For one-dimensional strategies, (iii) and (iv) can only happen near an evolutionary singularity. For multi-dimensional strategies, they can also happen if both strategies are sufficiently close to the same manifold orthogonal to the selection gradient vector field, but it is non-generic in the sense that with random mutations the probability goes to zero in the limit of small strategy differences.



**Fig. 3** Graphical illustration of resident-invader dynamics when the invader and the resident have similar but distinct strategies, generalized and adapted from Dercole and Geritz (2016, Fig.1). (i) Invasion without back-invasion implies substitution. (ii) The mutant cannot invade, but the resident can invade a population of the mutant, so that the resident stays the same. (iii) Mutual invasion leads to coexistence. (iv) Mutual exclusion because neither the mutant nor the resident can invade a population of the other.

same results for unstructured populations in a constant environment. Article I thus generalizes these results to a significantly larger class of models including structured populations and fluctuating environments.

One of the main uses of the classification of the resident-invader dynamics is that it enables us to answer the research questions **Q1**, **Q2** and **Q3** for small strategies difference and therefore, in particular, helps to interpret Pairwise Invasibility Plots (PIPs) in terms of possible evolutionary scenarios. Although for polymorphic resident populations and multi-dimensional strategies the construction of a PIP is impractical or even impossible, the classification can still be used for the same purpose. Previously, for structured populations and fluctuating environments such interpretation of PIPs was only conjectural, but now, in Article I, it has been given a rigorous foundation.

Article II investigates the evolution of the irreversible transition from a free-swimming state to an immobile sessile state as seen in many aquatic invertebrates. First, the population is modelled as a hypothetical microorganism onto the wall of a chemostat by using of the mechanistic modelling approach (refer to Section 3.1). The microorganism is assumed to have three different settling mechanisms involving competition for space on the wall: (*i*) purely exploitative competition where free-swimming individuals settle in vacant space only, (*ii*) mixed exploitative and interference competition where individuals attempt to settle in any place but fail and die if the space is already occupied, and (*iii*) mixed exploitative and interference competition, but now settling in occupied space is successful and the former occupant dies. Meanwhile, in the simplified environment of the chemostat, the input concentration of nutrients and the dilution rate of the tank are considered as the main environmental control variables. Second, the article studies the adaptive dynamics of the settling rate. The results reveal the impacts that certain environmental factors and ecological processes have on the evolutionary dynamics. More precisely, the environmental control variables and settling mechanisms have qualitatively different effects on the direction of evolution. Moreover, different fluctuation frequencies in the nutrient input have different effects on the long-term coexistence (in an evolutionary sense) of species with different settling rates. Finally, the article proposes some model-generated hypotheses concerning the evolution of aquatic invertebrates in different systematic groups, which may guide further empirical studies.

Article III investigates the evolution of the colonization rate of species in a patchy habitat when there is a trade-off with the competitive strength for individual patches. The model is formulated in the spirit of the existing competition-colonization models (Levins and Culver 1971; Calcagno et al. 2006), but in ad-

dition ours also includes ownership effects and random disturbance affecting the mortality rate. The results show that the strength of the trade-off, ownership effect and disturbance intensity all have a non-monotonic effect on the emergence of species diversity via evolutionary branching. In particular, intermediate disturbance promotes evolutionary branching and hence the emergence of polymorphisms on an evolutionary timescale. This result provides new evidence for the intermediate disturbance hypothesis (Connell 1978), namely, high richness in communities subject to an intermediate degree of disturbance. Another important result is that, in the strategy dynamics, random mutation steps may cause the transition of coevolutionary trajectories between neighbouring basins of attraction, which leads to various kinds of long-term evolutionary dynamics, including evolutionary branching-extinction cycles. This result suggests that we should pay attention to the role of random mutation steps (even they often have small phenotypic effects) when there are multiple evolutionary singularities in the strategy space.

## 2.4 New questions raised by the research

Article I extends the applicability of adaptive dynamics to fluctuating environments as well as structured populations by means of theoretical models. In specific models, Articles II and III reveal the effects of different environmental factors and ecological processes on the long-term evolution of phenotypic strategies. In light of these results, the dissertation demonstrates that adaptive dynamics is a powerful tool for untangling the environment-strategy relationships. The research presented in the dissertation raises various new research questions, both specific and more general. For the specific questions, I refer to the discussion sections of the respective articles. Here, I mention three new and general research questions:

- N1:** what is the resident-invader dynamics of similar strategies that takes the demographic stochasticity (due to the initially small population size of the invader) explicitly into account?
- N2:** what is the resident-invader dynamics of similar strategies when the population has a more general structure such as a continuous size or age distribution or a continuous distribution in space?
- N3:** what is the threshold behaviour of the random mutation-induced transition of coevolutionary trajectories between neighbouring basins of attraction when there are multiple evolutionary singularities in the strategy space?

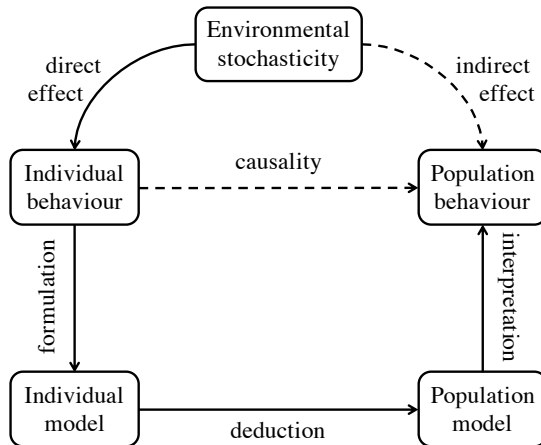
## Chapter 3

# Stochastic population models

This chapter describes how to incorporate environmental stochasticity into a population model.

A population is made up of individuals, and hence population dynamics is a consequence of the behaviour of the individuals. Environmental stochasticity, as a direct effect, affects individual behaviour such as birth, maturation, predation, competition, death, and so on. Fluctuations in individuals ultimately lead to the population change in size and structure in time and space, which is an indirect effect of environmental stochasticity (Fig. 4). From the perspective of modelling, a population model is deduced from the individual model that formulates individual events with associated event rates. For incorporating environmental stochasticity into a population model, researchers must identify how population parameters originate from various event rates and how environmental stochasticity affects the event rates. Only then it becomes possible to extract a specific relationship of different population parameters for explaining whether they vary independently or are related to one another in a specific way. Consequently, this way ensures that the introduction of environmental stochasticity is biologically interpretable, rather than casually adding noise terms to population parameters.

Next, I introduce the notion of the mechanistic modelling approach to derive the population model. Then I list some commonly used models that incorporate environmental stochasticity. Although environmental stochasticity is the focus



**Fig. 4** Diagram of modelling population in stochastic environments. Illustration by the author, inspired by the course “Stochastic Population Models” from Stefan A. H. Geritz.

of this dissertation, the modelling idea and approach are applicable to models with demographic stochasticity (see also Jagers 2010).

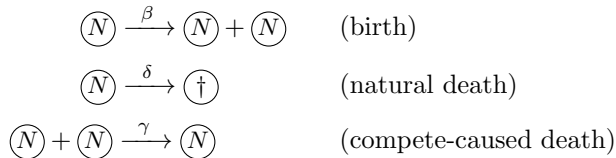
### 3.1 Mechanistic modelling

The basic principle of mechanistic modelling is to derive a population model from the individual level so that every model parameter is interpretable in terms of individuals’ behaviour (Geritz and Kisdi 2012). Before describing the behaviour of individuals, we must know which individual states are included. An individual may pass through various states during its lifespan (e.g., juvenile or reproductive states) or when interacting with another individual (e.g., prey or predatory states). A state transition is an event. Each event is characterised by an event rate, which is the occurrence probability of the event per unit of time. Next, these events can be formulated as a family of elementary reactions that describes the behaviour of individuals, which is so-called the individual model. Assuming a large number of individuals, we can apply the law of mass action to individual events to derive an equation that describes the change in population density. Collecting these equations forms a population model (Fig. 4). Now various event rates combine and end up as population parameters.

As an example, consider individuals have two states, living (denoted by  $\textcircled{N}$ )



and dead (denoted by  $\textcircled{\dagger}$ ). A living individual reproduces a new individual asexually at a rate  $\beta$ , and an individual dies naturally at a rate  $\delta$  or dies from competition at a rate  $\gamma$ . These individual events can be schematically represented as the following way.



Let  $n(t)$  denote the population density at time  $t$ . Applying the law of mass action to the events depicted above, the change in population density is given by

$$\frac{dn(t)}{dt} = (\beta - \delta)n(t) - \gamma n(t)^2. \quad (3.1)$$

The equation can be written as the well-known logistic equation

$$\frac{dn(t)}{dt} = rn(t) \left(1 - \frac{n(t)}{K}\right) \quad (3.2)$$

with parameters

$$\begin{aligned} r &= \beta - \delta, \\ K &= \frac{\beta - \delta}{\gamma}. \end{aligned} \quad (3.3)$$

Now I have derived the model of logistic growth for the population density by an underlying mechanism (i.e., interference competition), where every model parameter can be interpreted by the behaviour of individuals. Especially, the intrinsic growth rate  $r$  and the carrying capacity  $K$  are specific functions of the event rates  $\beta$ ,  $\delta$  and  $\gamma$ . When it comes to incorporating environmental stochasticity into the population model, we see that fluctuations in  $\beta$  and/or  $\delta$  cause the co-variation of  $r$  and  $K$ , but fluctuations in  $\gamma$  only affect  $K$ . Thus, the mechanistic modelling approach shows how to “add noise” to parameters in a meaningful way.

## 3.2 Types of noise

Environmental stochasticity essentially affects the event rates of individual behaviours and makes them fluctuate in time. Following this line, there are several

commonly used models in the literature for considering the impact of environmental stochasticity in population dynamics. For simplicity, the following introduction focuses on stochastic single-species, unstructured population models. Generalization to multi-species and structured population models is straightforward.

### ***Stochastic differential equations***

Consider a stochastic population model of the following form

$$\frac{dn(t)}{dt} = n(t)f(n(t), \theta(t)), \quad (3.4a)$$

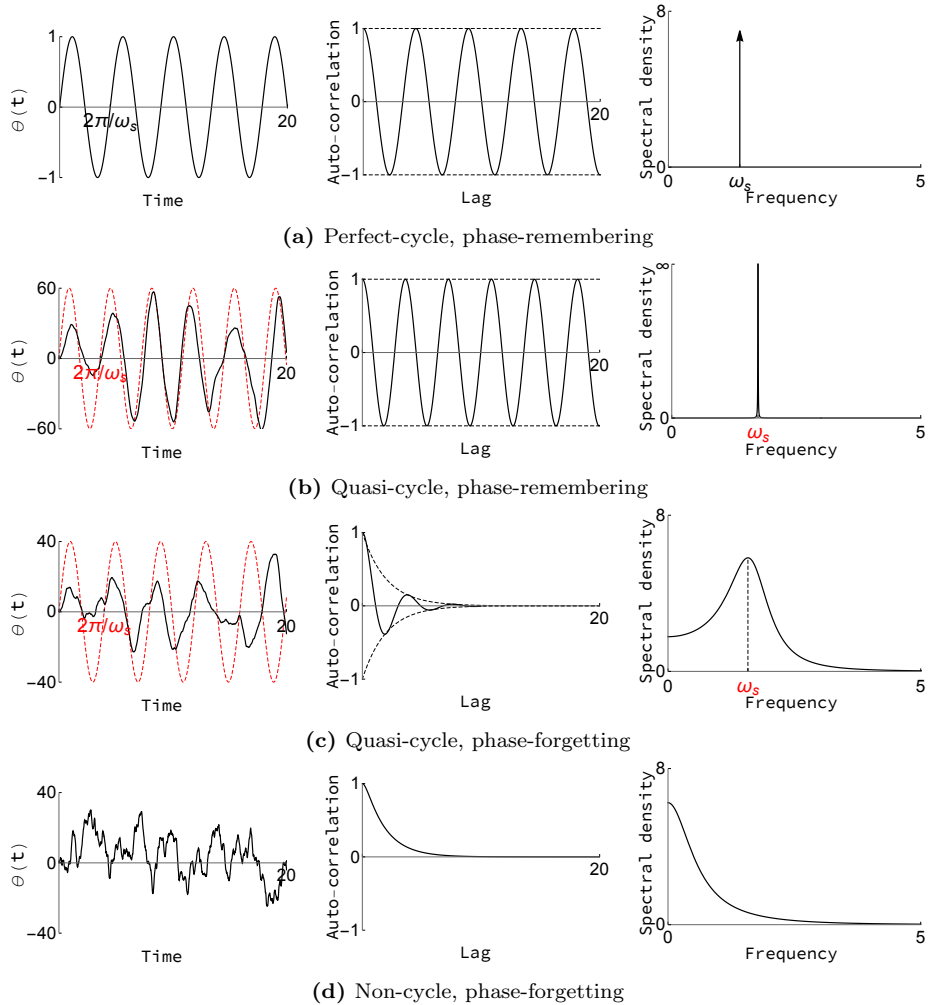
$$\frac{d\theta(t)}{dt} = A(\theta(t)) + B(\theta(t))\frac{dW(t)}{dt}, \quad (3.4b)$$

where  $W(t)$  is a standard Brownian motion and hence  $dW(t)/dt$  is the Gaussian white noise. In this form,  $\{\theta(t)\}_{t \geq 0}$  is a Markov process modelling environmental stochasticity where given the present environmental condition, the future is independent of the past. The Markov property is a natural consideration for many ecologically interpretable factors (see, e.g., Maruyama 1977; Ricciardi 1977; Arnold and Kliemann 1983). According to the knowledge of considered environmental factors, the  $\theta$  can be modelled as bounded noise and/or colored noise with finite correlation time (Kliemann 1983; d’Onofrio 2013; Caraballo and Han 2016; Spanio et al. 2017, see also Examples 4.1-4.3 shown in Article I). Notice that, process  $\{n(t)\}_{t \geq 0}$  is not Markovian, but joint process  $\{n(t), \theta(t)\}_{t \geq 0}$  is Markovian under weak assumptions (Arnold and Kliemann 1983).

In order to model phenomena that environmental fluctuations have memory and even are cyclic, namely, future environmental conditions depend on earlier ones (e.g., seasonal or tidal factors), the following second-order linear stochastic differential equation will be a good choice:

$$\frac{d^2\theta(t)}{dt^2} + a_1 \frac{d\theta(t)}{dt} + a_0\theta(t) = \sigma \frac{dW(t)}{dt}, \quad (3.4c)$$

where  $a_1 \geq 0$  is the damping coefficient,  $a_0 \geq 0$  is the restoring coefficient and  $\sigma \geq 0$  is the forcing intensity of the Gaussian white noise (Pandit and Wu 1983). By different parameter combinations,  $\theta$  can be modelled as different kinds of environmental noise in terms of the properties of phase-memory and cyclicity (Nisbet and Gurney 1982, Cai *in prep.*). Specifically, (i) when  $a_1 = 0$ ,  $a_0 \neq 0$  and  $\sigma = 0$ , the  $\theta$  is perfect-cyclic and phase-remembering (Fig. 5a, see also the



**Fig. 5** Plots of sample trajectory, auto-correlation function and spectral density of process  $\{\theta(t)\}_{t \geq 0}$  generated by (3.4c) with parameter combinations  $(a_1, a_0, \sigma) =$  (a)  $(0, 2, 0)$ , (b)  $(0, 3, 4)$ , (c)  $(1, 3, 4)$ , (d)  $(4, 2, 5)$ . In (a)-(c),  $\omega_s = \sqrt{a_0 - \frac{a_1^2}{2}}$  is the resonant frequency.

periodic fluctuations used in Article II); (ii) when  $a_1 = 0$ ,  $a_0 \neq 0$  and  $\sigma \neq 0$ , the  $\theta$  is quasi-cyclic and phase-remembering (Fig. 5b); (iii) when  $a_1^2 - 2a_0 < 0$ ,

$a_1 \neq 0$  and  $\sigma \neq 0$ , the  $\theta$  is quasi-cyclic and phase-forgetting (Fig. 5c); (iv) when  $a_1^2 - 2a_0 \geq 0$  and  $\sigma \neq 0$ , the  $\theta$  is no-cyclic and phase-forgetting (Fig. 5d).

When  $\theta$  is Gaussian white noise, (3.4) transforms into the form

$$\frac{dn(t)}{dt} = n(t)f_1(n(t)) + n(t)f_2(n(t))\frac{dW(t)}{dt}, \quad (3.5)$$

which is a special case of (3.4). Adding a white noise term to the system and then deriving out the form (3.5) is widely used in the literature (see, e.g., Beddington and May 1977; Turelli 1977; Braumann 2002; Imhof and Walcher 2005; Mao 2011; Schreiber et al. 2011; Evans et al. 2015; Hening and Nguyen 2018). As we see, in this form the infinity variance of Gaussian white noise might give rise to an unrealistic consideration. Instead, following the work by Turelli (1977), (3.5) is best viewed as analytically tractable approximations of stochastic difference equations, which are more realistic. The model used in Article III belongs to this category. Unlike the process  $\{n(t)\}_{t \geq 0}$  in the form of (3.4a), the  $\{n(t)\}_{t \geq 0}$  in (3.5) is Markovian.

### *Piecewise deterministic Markov processes*

Environmental conditions may switch between some distinct states and random jump at points in time (hence have stochastic durations). Once the environment is determined, the population dynamics are governed by ordinary differential equations. The piecewise deterministic Markov processes provide an approach to modelling this kind of phenomena.

Consider a stochastic population model of the following form

$$\frac{dn(t)}{dt} = n(t)f(n(t), \theta(t)) \quad (3.6a)$$

$$\begin{aligned} & \mathbb{P}\{\theta(t + \Delta) = j | \theta(t) = i, n(s), \theta(s), s \leq t\} \\ &= \begin{cases} q_{ij}\Delta + \mathcal{O}(\Delta) & \text{if } i \neq j \\ 1 + q_{ii}\Delta + \mathcal{O}(\Delta) & \text{if } i = j \end{cases} \end{aligned} \quad (3.6b)$$

where  $\{\theta(t)\}_{t \geq 0}$  is a continuous-time Markov process taking values in discrete state space  $\mathcal{E} = \{1, \dots, k\}$  that keeps track of the environment. In (3.6b),  $q_{ij}$  is the transition rate in unit time from environments  $i$  to  $j \in \mathcal{E}$  and  $q_{ii} = -\sum_{j \neq i} q_{ij}$ . The matrix  $Q = (q_{ij})_{i, j \in \mathcal{E}}$  is assumed to be irreducible. Many literature use this form to study the population dynamics in variable environments with a specific switching-mechanism (Litchman and Klausmeier 2001; Kussell

and Leibler 2005; Tyson and Lutscher 2016; Benaïm and Lobry 2016; Hening and Nguyen 2020).

Alternatively, the population dynamics may in turn affect the environment by influencing the transition rates between different environmental states, namely,  $q_{ij}$  becomes a function of  $n(t)$  for each  $i, j \in \mathcal{E}$ . Such a feedback loop well captures the interaction of the population and the variable environments (see, e.g., Cuddington et al. 2009; Staver and Levin 2012). Regardless of whether the transition rates are density-dependent or density-independent, the joint process  $\{n(t), \theta(t)\}_{t \geq 0}$  is Markovian (Davis 1984).

### ***Other possible types***

In addition to these general models, there are other possible types to model complex phenomena. For instance, a combination of the above two models transforms into the so-called stochastic differential equations with Markovian switching. This kind of models is similar to piecewise deterministic Markov processes, but now the population dynamics are given by stochastic differential equations (Mao and Yuan 2006). This form captures the environmental stochasticity that involves the fluctuation between different environments (seasonal climate) and the fluctuation within each environment (daily weather) (see, e.g., Zhu and Yin 2009; Greenhalgh et al. 2016; Hening and Li 2020). Another scenario might be that environmental fluctuations happen in a timescale much different from that of the population dynamics. Thus, stochastic fast-slow models can be used to describe these phenomena (see, e.g., Freidlin and Wentzell 2012; O'Regan 2018; Hastings et al. 2018). This list is not exhaustive, and new types may emerge in specific ecological-evolutionary studies.

The conclusions of Article I apply to all the above-mentioned types of noise.



# Chapter 4

## Adaptive dynamics

This chapter gives an introduction to the approach of adaptive dynamics, which is a central approach of the dissertation in investigating the long-term evolution of phenotypic strategies.

### 4.1 Background

Adaptive dynamics is a mathematical and conceptual framework developed during the 1990s for understanding the long-term evolutionary consequences of small mutations in phenotypic strategies. Individual strategies affect the population dynamics, and the population dynamics selects which strategies prevail and which do not. Selection emerges from the population dynamics rather than being the result of applying a predetermined notion of fitness. Thus, adaptive dynamics explicitly links long-term evolutionary phenomena to population dynamics. This is possibly the most important difference with other approaches such as population genetics and most applications of evolutionary game theory, which lack a strong population dynamical basis.

The approach of adaptive dynamics uses the following four basic assumptions (Geritz et al. 1998; Geritz and Gyllenberg 2005). First, individuals reproduce asexually. This means that the offspring inherit the parental phenotypic strategy. Second, mutations are rare so that the resident population has reached its attractor before the next mutant appears. Thereby, there is a separation of the slower mutational time scale from the faster population dynamical time scale. Third, mutations are of small phenotypic effect. Fourth, the mutation

population is initially rare and hence the ecological environment generated by the resident population affects the mutant but not the other way around. Under these assumptions, the analysis starts from the invasion fitness of mutants measured by the initial growth rate of the mutant or from a proxy for the invasion fitness (e.g., the basic reproduction number measured by the expected total number of offspring that a mutant individual produces in its lifetime). Determining the invasion fitness or its proxy may sometimes be difficult, but once it can be determined, the approach of adaptive dynamics is readily applied and is independent of the model structure.

The approach of adaptive dynamics provides a handy toolkit for evolutionary studies, with special emphases on the properties of evolutionary singularities, the origin and divergence of new lineages, and the evolutionary outcomes.

For illustrating the approach of adaptive dynamics, the following brief introduction focuses on scalar-valued strategies in unstructured populations with dynamics described by the model (2.1). More comprehensive introductions can be found in Diekmann (2004), Brännström et al. (2013) and Kisdi (2020), which also include an overview of literature that extends the approach to more complex ecological settings (e.g., sexual reproduction, spatial structures, function-valued strategies). For understanding the probabilistic foundation of adaptive dynamics, I recommend the work by Champagnat et al. (2006). To track the theoretical advancements and the applications in specific ecological-evolutionary problems, I recommend the continually updating web page (<https://www.mv.helsinki.fi/home/kisdi/addyn.htm>) maintained by Éva Kisdi.

## 4.2 General framework

### *Resident population dynamics*

Consider a resident system with dynamics given by (2.1), where the resident densities  $(n_1(t), \dots, n_k(t))$  together with the respective strategies  $(x_1, \dots, x_k)$  is called the resident population, and where  $e(t)$  describes the feedback environment interacting with the resident population, and where  $\theta(t)$  captures the external factors influencing the resident population as well as the feedback environment. Since mutation happens on a slower time scale, the system has sufficient time to reach a dynamical attractor. Such an attractor can be an equilibrium, a cycle, or an invariant distribution—on an appropriate state space but excluding the extinction set of the population (refer to Schreiber et al. 2011 and see also Article I).



## *Invasion fitness*

From now on, let  $\mathbf{x}$  denote the collection of strategies  $x_1, \dots, x_k$  and let  $\mathbf{n}(t)$  denote the collection of corresponding population densities  $n_1(t), \dots, n_k(t)$  at time  $t$ . The invasion fitness of an initially rare mutant with strategy  $y$  in the environment generated by the resident system at its dynamical attractor is

$$\mathcal{S}_{\mathbf{x}}(y) = \lim_{t \rightarrow +\infty} \frac{1}{t} \int_0^t f(y, e(s), \theta(s)) ds, \quad (4.1)$$

where the function  $f$  is the *per capita* growth rate of individuals with strategy  $y$  in the environment  $(e(s), \theta(s))$  (Metz et al. 1992; Ferriere and Gatto 1995).

When the dynamical attractor of the resident system is an equilibrium state  $(\hat{\mathbf{n}}, \hat{e}, \hat{\theta})$ , then the invasion fitness is explicitly given by

$$\mathcal{S}_{\mathbf{x}}(y) = f(y, \hat{e}, \hat{\theta}). \quad (4.2)$$

If the dynamical attractor corresponds to a periodic orbit  $(\tilde{\mathbf{n}}(s), \tilde{e}(s), \tilde{\theta}(s))$  with period  $T$ , then the invasion fitness reduces to

$$\mathcal{S}_{\mathbf{x}}(y) = \frac{1}{T} \int_0^T f(y, \tilde{e}(s), \tilde{\theta}(s)) ds. \quad (4.3)$$

The periodic environments treated in Article II belong to this category. If the dynamical attractor corresponds to an invariant probability measure  $\mu$  on a state space  $\bar{\mathcal{Z}}$ , then invasion fitness

$$\mathcal{S}_{\mathbf{x}}(y) = \int_{\bar{\mathcal{Z}}} f(y, e, \theta) \mu(de, d\theta) \quad \mu\text{-almost surely.} \quad (4.4)$$

The ergodic environments treated in Articles I and III belong to this category.

Once the invasion fitness is determined, the mutant dies out if it has a negative invasion fitness. Conversely, if the mutant has a positive invasion fitness, then it may spread in the resident environment (but extinction is still possible due to the demographic stochasticity in small population sizes). Since all resident subpopulations have zero long-term growth,

$$\mathcal{S}_{\mathbf{x}}(x_i) = 0 \quad (4.5)$$

for all  $i = 1, \dots, k$ , where the equal-sign holds in a stochastic sense if the scenario in (4.4) happens.

For a large class of deterministic, unstructured population models, the population dynamical outcomes of an invasion event are determined by the invasion criteria alone (Geritz 2005; Dercole and Geritz 2016). Article I and the supplementary material extend and generalize this result to non-equilibrium resident population dynamics, resident dynamics with environmental stochasticity, and class-structured population models. Typically, if a mutant can invade the resident but not the other way around, the mutant will oust the resident and take over the population, i.e., the “invasion implies substitution”-principle. However, if the resident can invade back so that it is protected against extinction, then the resident and the mutant eventually live together, i.e., the “mutual invasion implies coexistence”-principle. Therefore, invasion outcomes can be predicted directly from the signs of invasion fitnesses. For scalar-valued strategies, the sign plot is visible, i.e., the PIP and MIP (refer to Figs. 6a and 6c).

### *Selection gradient*

The direction of evolution is determined by the selection gradient:

$$\begin{aligned} \mathcal{G}(\mathbf{x}) &= (\mathcal{G}_i(\mathbf{x}))_{i=1, \dots, k}^\top \\ &= \left( \left. \frac{\partial \mathcal{S}_x(y)}{\partial y} \right|_{y=x_1}, \dots, \left. \frac{\partial \mathcal{S}_x(y)}{\partial y} \right|_{y=x_k} \right)^\top \end{aligned} \quad (4.6)$$

where the  $i$ -th component  $\mathcal{G}_i$  is the partial derivative  $\partial \mathcal{S}_x(y)/\partial y$  of the invasion fitness evaluated at resident  $x_i$ . A point in the strategy space for which all components of the selection gradient become zero simultaneously (and hence not directional change) is called an evolutionarily singular coalition. For one-dimensional strategy dynamics, such a point is called an evolutionarily singular strategy.

### *Monomorphic evolution*

For the evolution in a monomorphic population, a singularity  $x^*$  is said to be an Evolutionarily Stable Strategy (ESS) if the invasion fitness at this point is local maximum, i.e., the second-order derivative of the invasion fitness

$$\left. \frac{\partial^2 \mathcal{S}_x(y)}{\partial y^2} \right|_{y=x=x^*} < 0. \quad (4.7)$$

The definition of an ESS has its root in the evolutionary game theory (Maynard Smith 1982) and is a global concept, i.e., the ESS is immune to invasion by any other strategy. However, in the context of adaptive dynamics, an ESS is a local concept, i.e., such a strategy can not be invaded by any nearby mutant strategies but is possible for sufficiently different mutant strategies if large mutation steps are accessible.

A singularity  $x^*$  is called convergence stable if

$$\left. \frac{\partial^2 \mathcal{S}_x(y)}{\partial y^2} \right|_{y=x=x^*} - \left. \frac{\partial^2 \mathcal{S}_x(y)}{\partial x^2} \right|_{y=x=x^*} < 0, \quad (4.8)$$

which is an evolutionary attractor in the strategy space. Conversely, the  $x^*$  becomes an evolutionary repeller if it is not convergence stable.

When a singularity is both convergence and evolutionarily stable, it is a Continuously Stable Strategy (CSS, Eshel and Motro 1981; Eshel 1983) and hence an endpoint of the evolutionary process. However, if a singularity is convergence stable but not evolutionarily stable, it is a Branching Point (BP, Geritz et al. 1998) in the strategy space. When the evolution gradually approaches a BP, the initially monomorphic population inevitably sooner or later becomes dimorphic.

Central to the adaptive dynamics of evolving strategies is finding evolutionary singularities. This has to check many different combinations of model parameters and may be time-consuming and goalless. Critical Function Analysis (de Mazancourt and Dieckmann 2004; Bowers et al. 2005; Geritz et al. 2007) is a powerful method for finding singularities and determining the conditions for desired evolutionary outcome. The method is to construct a family of critical functions based on the biological assumption that the evolving strategy is traded off with one other model parameter (see also Kisdi (2006) for the case of coevolving species and Kisdi (2015) for the case of multiple trade-offs). The conditions for the desired outcome can be determined directly. Once a specific trade-off function is given, the plot of the critical functions provides a visual way to identify singularities and their convergence stability. Article III also applies this method to find BPs.

### *Polymorphic evolution*

For the evolution in a polymorphic population, an evolutionarily singular coalition  $\mathbf{x}^* = (x_1^*, \dots, x_k^*)$  is said to be evolutionarily stable if and only if all its

constituent strategies are ESS, i.e., satisfying

$$\left. \frac{\partial^2 \mathcal{S}_{\mathbf{x}}(y)}{\partial y^2} \right|_{y=x_i^*, \mathbf{x}=\mathbf{x}^*} < 0 \quad (4.9)$$

for all  $i$ . Unlike the convergence stability in monomorphic evolution that depends solely on the selection gradient, the convergence of a singular coalition is complicated because it in addition also depends on mutation rates and step sizes in the various resident strategies. There are several concepts of convergence stability but depending on the underlying assumptions concerning mutation rates and step sizes (Leimar 2001, 2009). In fact, the local convergence stability of a singular coalition is determined by the canonical equation shown below and normally has to resort to numerical analysis in case studies.

A singular coalition is an endpoint of the evolution process if it is attainable through gradual evolution and is evolutionarily stable, whereas further evolutionary branching occurs if it lacks evolutionary stability in at least one direction.

### ***Evolutionary path***

In the constant environment (i.e., the dynamical attractor of the resident system corresponds to equilibrium state), the evolutionary path of multispecific strategies in the strategy space can be described by the following ordinary differential equations

$$\frac{dx_i}{dt} = \frac{1}{2} \mu_i(x_i) \sigma_i^2(x_i) \hat{n}_i(\mathbf{x}) \mathcal{G}_i(\mathbf{x}), \quad i = 1, \dots, k, \quad (4.10)$$

where  $\mu_i(x_i)$  is the mutation probability per birth event in the strategy value  $x_i$ ,  $\sigma_i^2(x_i)$  is the variance of the mutation step-size distribution in the strategy value  $x_i$ ,  $\hat{n}_i(\mathbf{x})$  is the equilibrium population density of the resident population of strategy  $x_i$  in the community characterized by  $\mathbf{x}$ ,  $\mathcal{G}_i(\mathbf{x})$  is the selection gradient in  $x_i$ -direction, and the factor 1/2 comes from the assumption of symmetric mutation distribution and the linear approximation applying in the half strategy space. This is so-called the canonical equation of adaptive dynamics, which is the deterministic approximation of the stochastic mutation process under the assumption of sufficiently small mutations (Dieckmann and Law 1996; Champagnat et al. 2001). The first four terms in the right hand side of (4.10) are all non-negative and jointly describe the rate of evolutionary change in the  $i$ -th strategy. Durinx et al. (2008) extend the applicability of this canonical equation to general physiologically structured population models with multiple birth states.

In the case of arbitrary ergodic environments, both the number of births and the invasion probability have to be averaged over all possible environmental conditions. A general form of the canonical equation for this case is derived in Ripa and Dieckmann (2013):

$$\frac{dx_i}{dt} = \frac{1}{2} \mu_i(x_i) \sigma_i^2(x_i) \frac{\mathbb{E}[b_i(\mathbf{x})]}{\mathbb{E}[n_i^{-1}(\mathbf{x}) b_i(\mathbf{x})]} \mathcal{G}_i(\mathbf{x}), \quad i = 1, \dots, k, \quad (4.11)$$

where  $b_i(\mathbf{x})$  is the *per capita* birth rate of the resident population with strategy  $x_i$  in the community characterized by  $\mathbf{x}$ ,  $n_i(\mathbf{x})$  is the corresponding population density, and  $\mathbb{E}[\cdot]$  indicates the expectation over all possible environmental conditions. There are several equivalent forms of (4.11) following from the fact that for resident populations,  $\ln(n_i(t))$  and  $n_i^{-1}(t)$  have a long-term growth rate of zero.

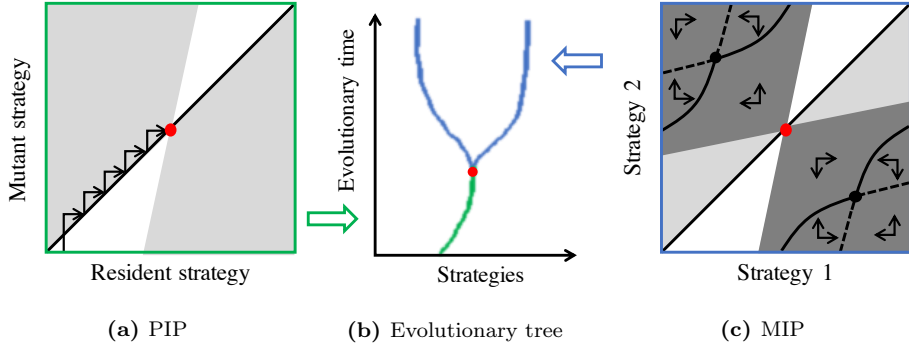
In addition to these general forms, Metz et al. (2016) provides the form of the canonical equation of adaptive dynamics for life history models, where the strategy is a function of the state of the individual. In particular, they treat the canonical equation in periodic environments.

An important phenomena is that of multiple evolutionary attractors in the polymorphic evolution. If there exists several singularities and each has own basin of attraction, random mutations with small but non-zero steps may cause the transition of evolutionary paths between neighbouring basins. This transition behaviour can be analyzed through a diffusion approximation of the stochastic mutation process developed by Champagnat et al. (2001). Article III provides an example for which an evolutionary path starting from the vicinity of BP will visit different attraction basins with positive probabilities as was suggested by the results of Champagnat's (2003) works, which can lead to various kinds of long-term evolutionary dynamics.

### ***Key graphics in adaptive dynamics***

Fig. 6a is the Pairwise Invasibility Plot (PIP, Matsuda 1985; van Tienderen and de Jong 1986). In the light grey areas, the mutant can invade the resident; in the empty areas, invasion is impossible. The arrows indicate gradual evolution proceeding by invasion and substitution of mutants. The red point marks the singularity. In this example, the singularity is convergence stable but not evolutionarily stable and hence a branching point.

Fig. 6c is the Mutual Invasibility Plot (MIP) as the combination of the PIP and the diagonal-reversed PIP. In the dark grey areas, any combination



**Fig. 6** Key graphics in adaptive dynamics.

of two strategies are mutually invisable and hence protected dimorphism. The arrows obtained from the canonical equation indicate the direction of small evolutionary steps. The lines, inside the coexistence area, are the adaptive isoclines that indicate selection gradient vanishes in one of the two components, where the solid lines correspond to local fitness maxima of the mutant and the dashed lines correspond to local fitness minima of the mutant. The black points, intersections of isoclines, mark the evolutionarily singular coalitions and always occur in reciprocal pairs as the diagonal symmetry. In this example, the singular coalition is both convergence and evolutionarily stable.

Together with the PIP and MIP, Fig. 6b is a simulated evolutionary tree that indicates the adaptive movement of evolving strategies. The green part corresponds to the path of monomorphic evolution. After reaching the branching point, the blue part shows the coevolutionary path of the two directions in the strategy space.

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