Interim Report   **IR-05-074**

Multi-type Branching Processes and Adaptive Dynamics of Structured Populations
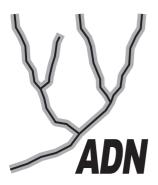
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December 2005

IIASA STUDIES IN ADAPTIVE DYNAMICS   NO. 106

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No. 5 Law R, Marrow P, Dieckmann U: *On Evolution under Asymmetric Competition.* IIASA Working Paper WP-96-003 (1996). Evolutionary Ecology 11:485-501 (1997).

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No. 7 Ferrière R, Gatto M: *Lyapunov Exponents and the Mathematics of Invasion in Oscillatory or Chaotic Populations.* Theoretical Population Biology 48:126-171 (1995).

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No. 13 Heino M, Metz JAJ, Kaitala V: *Evolution of Mixed Maturation Strategies in Semelparous Life-Histories: The Crucial Role of Dimensionality of Feedback Environment.* IIASA Working Paper WP-96-126 (1996). Philosophical Transactions of the Royal Society of London Series B 352:1647-1655 (1997).

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No. 22 Law R, Dieckmann U: *Symbiosis Without Mutualism and the Merger of Lineages in Evolution.* IIASA Interim Report IR-97-074 (1997). Proceedings of the Royal Society of London Series B 265:1245-1253 (1998).

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No. 28 Kisdi É: *Evolutionary Branching Under Asymmetric Competition.* IIASA Interim Report IR-98-045 (1998). Journal of Theoretical Biology 197:149-162 (1999).

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No. 34 Mathias A, Kisdi É: *Evolutionary Branching and Coexistence of Germination Strategies.* IIASA Interim Report IR-99-014 (1999).

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No. 36 Metz JAJ, Gyllenberg M: *How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies.* IIASA Interim Report IR-99-019 (1999). Proceedings of the Royal Society of London Series B 268:499-508 (2001).

No. 37 Gyllenberg M, Metz JAJ: *On Fitness in Structured Metapopulations.* IIASA Interim Report IR-99-037 (1999). Journal of Mathematical Biology 43:545-560 (2001).

No. 38 Meszéna G, Metz JAJ: *Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality.* IIASA Interim Report IR-99-045 (1999).

No. 39 Kisdi É, Geritz SAH: *Evolutionary Branching and Sympatric Speciation in Diploid Populations.* IIASA Interim Report IR-99-048 (1999).

No. 40 Ylikarjula J, Heino M, Dieckmann U: *Ecology and Adaptation of Stunted Growth in Fish.* IIASA Interim Report IR-99-050 (1999). Evolutionary Ecology 13:433-453 (1999).

No. 41 Nowak MA, Sigmund K: *Games on Grids.* IIASA Interim Report IR-99-038 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 135-150 (2000).

No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation.* IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).

No. 43 Kisdi É, Jacobs FJA, Geritz SAH: *Red Queen Evolution by Cycles of Evolutionary Branching and Extinction.* IIASA Interim Report IR-00-030 (2000). Selection 2:161-176 (2001).

No. 44 Meszéna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ: *Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics.* IIASA Interim Report IR-00-039 (2000). Selection 2:193-210 (2001).

No. 45 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ: *Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity.* IIASA Interim Report IR-00-035 (2000). Journal of Evolutionary Biology 16:143-153 (2003).

No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions.* IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).

No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model.* IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).

No. 48 Gyllenberg M, Parvinen K, Dieckmann U: *Evolutionary Suicide and Evolution of Dispersal in Structured Metapopulations.* IIASA Interim Report IR-00-056 (2000). Journal of Mathematical Biology 45:79-105 (2002).

No. 49 van Dooren TJM: *The Evolutionary Dynamics of Direct Phenotypic Overdominance: Emergence Possible, Loss Probable.* IIASA Interim Report IR-00-048 (2000). Evolution 54:1899-1914 (2000).

No. 50 Nowak MA, Page KM, Sigmund K: *Fairness Versus Reason in the Ultimatum Game.* IIASA Interim Report IR-00-57 (2000). Science 289:1773-1775 (2000).

No. 51 de Feo O, Ferrière R: *Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling.* IIASA Interim Report IR-00-074 (2000). International Journal of Bifurcation and Chaos 10:443-452 (2000).

No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola.* IIASA Interim Report IR-01-018 (2001). Oikos 94:525-532 (2001).

No. 53 Sigmund K, Hauert C, Nowak MA: *Reward and Punishment in Minigames.* IIASA Interim Report IR-01-031 (2001). Proceedings of the National Academy of Sciences of the USA 98:10757-10762 (2001).

No. 54 Hauert C, De Monte S, Sigmund K, Hofbauer J: *Oscillations in Optional Public Good Games.* IIASA Interim Report IR-01-036 (2001).

No. 55 Ferrière R, Le Galliard J: *Invasion Fitness and Adaptive Dynamics in Spatial Population Models.* IIASA Interim Report IR-01-043 (2001). Clobert J, Dhondt A, Danchin E, Nichols J (eds): Dispersal, Oxford University Press, pp. 57-79 (2001).

No. 56 de Mazancourt C, Loreau M, Dieckmann U: *Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism.* IIASA Interim Report IR-01-053 (2001). The American Naturalist 158:109-123 (2001).

No. 57 Claessen D, Dieckmann U: *Ontogenetic Niche Shifts and Evolutionary Branching in Size-Structured Populations.* IIASA Interim Report IR-01-056 (2001). Evolutionary Ecology Research 4:189-217 (2002).

No. 58 Brandt H: *Correlation Analysis of Fitness Landscapes.* IIASA Interim Report IR-01-058 (2001).

No. 59 Dieckmann U: *Adaptive Dynamics of Pathogen-Host Interacations.* IIASA Interim Report IR-02-007 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 39-59 (2002).

No. 60 Nowak MA, Sigmund K: *Super- and Coinfection: The Two Extremes.* IIASA Interim Report IR-02-008 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 124-137 (2002).

No. 61 Sabelis MW, Metz JAJ: *Taking Stock: Relating Theory to Experiment.* IIASA Interim Report IR-02-009 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management, Cambridge University Press, Cambridge, UK, pp. 379-398 (2002).

No. 62 Cheptou P, Dieckmann U: *The Evolution of Self-Fertilization in Density-Regulated Populations .* IIASA Interim Report IR-02-024 (2002). Proceedings of the Royal Society of London Series B 269:1177-1186 (2002).

No. 63 Bürger R: *Additive Genetic Variation Under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study.* IIASA Interim Report IR-02-013 (2002). Theoretical Population Biology 61:197-213 (2002).

No. 64 Hauert C, De Monte S, Hofbauer J, Sigmund K: *Volunteering as Red Queen Mechanism for Co-operation in Public Goods Games.* IIASA Interim Report IR-02-041 (2002). Science 296:1129-1132 (2002).

No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition.* IIASA Interim Report IR-02-053 (2002). Evolution 56:1081-1090 (2002).

No. 66 Dercole F, Rinaldi S: *Evolution of Cannibalistic Traits: Scenarios Derived from Adaptive Dynamics.* IIASA Interim Report IR-02-054 (2002). Theoretical Population Biology 62:365-374 (2002).

No. 67 Bürger R, Gimelfarb A: *Fluctuating Environments and the Role of Mutation in Maintaining Quantitative Genetic Variation.* IIASA Interim Report IR-02-058 (2002). Genetical Research 80:31-46 (2002).

No. 68 Bürger R: *On a Genetic Model of Intraspecific Competition and Stabilizing Selection.* IIASA Interim Report IR-02-062 (2002). Amer. Natur. 160:661-682 (2002).

No. 69 Doebeli M, Dieckmann U: *Speciation Along Environmental Gradients.* IIASA Interim Report IR-02-079 (2002). Nature 421:259-264 (2003).

No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model.* IIASA Interim Report IR-02-078 (2002). SIAM Journal on Applied Mathematics 63:1378-1391 (2003).

No. 71 Le Galliard J, Ferrière R, Dieckmann U: *The Adaptive Dynamics of Altruism in Spatially Heterogeneous Populations.* IIASA Interim Report IR-03-006 (2003). Evolution 57:1-17 (2003).

No. 72 Taborsky B, Dieckmann U, Heino M: *Unexpected Discontinuities in Life-History Evolution under Size-Dependent Mortality.* IIASA Interim Report IR-03-004 (2003). Proceedings of the Royal Society of London Series B 270:713-721 (2003).

No. 73 Gardmark A, Dieckmann U, Lundberg P: *Life-History Evolution in Harvested Populations: The Role of Natural Predation.* IIASA Interim Report IR-03-008 (2003). Evolutionary Ecology Research 5:239-257 (2003).

No. 74 Mizera F, Meszéna G: *Spatial Niche Packing, Character Displacement and Adaptive Speciation Along an Environmental Gradient.* IIASA Interim Report IR-03-062 (2003). Evolutionary Ecology Research 5:363-382 (2003).

No. 75 Dercole F: *Remarks on Branching-Extinction Evolutionary Cycles.* IIASA Interim Report IR-03-077 (2003). Journal of Mathematical Biology 47:569-580 (2003).

No. 76 Hofbauer J, Sigmund K: *Evolutionary Game Dynamics.* IIASA Interim Report IR-03-078 (2003). Bulletin of the American Mathematical Society 40:479-519 (2003).

No. 77 Ernande B, Dieckmann U, Heino M: *Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation.* IIASA Interim Report IR-03-058 (2003). Proceedings of the Royal Society of London Series B-Biological Sciences 271:415-423 (2004).

No. 78 Hanski I, Heino M: *Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes.* IIASA Interim Report IR-03-028 (2003). Theoretical Population Biology 63:309-338 (2003).

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No. 86 Vukics A, Asbóth J, Meszéna G: *Speciation in Multidimensional Evolutionary Space.* IIASA Interim Report IR-04-028 (2004). Physical Review 68:041-903 (2003).

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No. 97 Hauert C, Haiden N, Sigmund K: *The Dynamics of Public Goods.* IIASA Interim Report IR-04-086 (2004). Discrete and Continuous Dynamical Systems - Series B 4:575-587 (2004).

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No. 106 Durinx M, Metz JAJ: *Multi-type Branching Processes and Adaptive Dynamics of Structured Populations.* IIASA Interim Report IR-05-065 (2005). Haccou P, Jager P, Vatutin V (eds): Branching Processes: Variation, Growth and Extinction of Populations, Cambridge University Press, Cambridge, UK, pp. 266-278 (2005).

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Contents

Multi-type Branching Processes and Adaptive Dynamics of Structured Populations

M. Durinx and J.A.J. Metz

1   Introduction

Adaptive dynamics deals with the consequences of the repeated establishment of rare mutants in environments set by large equilibrium populations of residents. It studies which mutants can potentially invade, which successful invasions lead to the demise of the original residents, and what the evolutionary outcome can be of a prolonged series of such substitution events (Metz *et al.* 1996). The main assumptions are

rare mutations: the community dynamics has settled on an attractor between mutation events, hence the ecological and evolutionary time scales are separated.

initially rare mutants: the well-mixed resident populations have a large size, while the mutant's population starts up from a single mutant.
The assumed magnitude of the resident population makes its dynamics deterministic, whereas the rarity of the invading mutant induces a strong stochastic effect.

small mutational steps: mutants must be similar to one of the residents, to allow sensible topological and geometrical inferences.

We restrict in this section the postulate of deterministic resident dynamics even further, to the case where its attractors are fixed points. Combined with the time scale supposition, this allows one to regard the residents as stationary on the ecological time scale.

The main attraction of this restrictive set of assumptions is that it allows the construction of a mathematically consistent framework for studying the possible patterns of evolutionary outcomes, based on a precise if not always equally realistic foundation of mechanistic biological reasoning.

The traits that we study as being under evolutionary control through mutation and selection, must be thought of as parameters that govern the life history

of individuals. Each resident population consists of a large number of individuals sharing a characteristic trait. Several such populations, with different traits or trait values, make up the community of residents. In this environment, a single newborn individual may have an advantageous mutation, giving rise to an initially small mutant population. In the long run, the presence of the newcomers affects the fitness and thereby possibly the persistence of the resident populations; this interplay lets evolution shape the species of the community.

The study of the evolutionary dynamics can be broadly divided in two categories. Firstly, away from special points called singularities (as defined in 2), directional selection acts. Then the dictum *"invasion implies fixation"* holds, which means that any persistent mutant will drive its ancestral resident to extinction. This property is proved in Geritz *et al.* (2002) on the assumption that the population dynamical attractors are sufficiently well-behaved. Through this mechanism, the standing diversity remains the same since the emergence of a successful new type implies the disappearance of an older type.

One way of failing to be well-behaved is to have a qualitative change in the pattern of the population dynamics (known in dynamical systems theory as a bifurcation). The appearance of a mutant then may lead to the demise of not only the resident that spawned it, but also other resident types, thereby reducing the diversity present in the community. The more extreme cases involve evolutionary suicide, where a sequence of substitution events can drive the entire community to extinction (e.g. Gyllenberg and Parvinen 2001).

Secondly, at singularities, the attractiveness of adaptive dynamics as an evolutionary framework is revealed. One of the categories a singularity can belong to, is that of the classic-but-inappropriately-named *evolutionary stable strategy (ESS)* known from evolutionary game theory (Maynard Smith 1982). However, there are other naturally occurring types of singularities. Foremost, the *branching point*, an attracting singularity in the proximity of which the population dynamics exerts disruptive selection. This selection acts such that a newly established mutant does not send its progenitor to kingdom come. Instead the two coexisting types will diverge further and further, so that soon they will sit on opposite sides of the singularity. When plotting the resident strategies against evolutionary time, one sees the "branches" that gave the singularity its name. This splitting of genetical lines has an obvious appeal as a model for (the initiation of) speciation. For a deeper understanding we refer to the book on adaptive speciation (Dieckmann *et al.* 2004) in this series.

In this section, we only consider evolution at a distance from singularities. Under such a regime of directional selection, one can estimate the rate of trait substitutions as Dieckmann and Law (1996) did, formulating the *"canonical equation of adaptive dynamics"*. We will show how Durinx *et al.* (in prep.) extend this equation to physiologically structured populations. In particular, we sketch how the speed of evolution is assessed from the underlying branching process of the invasion dynamics.

2 The invasion fitness

The main tool of adaptive dynamics is the *invasion fitness function*. By definition this is the long-term average per capita growth rate of a rare type (the *invader*) in an equilibrium community of a given set of types (the *residents*). Thus it is the Malthusian parameter of the invader. One sees that any resident type cast in the role of invader always has zero invasion fitness, since it will on average neither grow nor diminish in abundance. An invader with a negative fitness will never gain a foothold in the given community, whereas a positive fitness implies a positive probability of establishment. As this concerns a stochastic process with a very small amount of invaders, even a positive average growth rate will not prevent extinction in a fair amount of cases: establishment must be studied as the outcome of a branching process.

The assumption of small mutational steps lets the *mutants* differ but slightly from one of the resident types. The tacit biological suggestion is that any mutation with a large effect would be detrimental due to pleiotropy, thus guaranteeing a truncation of the effective mutation distribution.

When a mutant has a positive invasion fitness, but due to stochasticity its attempt at establishment fails, this is not the end. Evolution can bide its time and a later occurring similar mutation may get established due to better luck. In the simplest setting, the probability of success for single invasion attempts only affects the speed of evolution rather than its endpoint. However, in polymorphic populations or higher dimensional strategy spaces, the speed, direction and outcome can all be affected.

The *strategy, trait value* or simply *trait* of an individual denotes its particular set of values for the parameters that are under evolutionary control; this can be a vector or just a single scalar value. A *polymorphic* community has individuals with differing traits. We only consider cases where there is a finite number of strategies present. If we lump together all individuals with an identical strategy, they are collectively referred to as a *type, population*, or *species*. Clearly, this last term is very loose at this point, not implying any well-defined biological species concept. For simplicity, we will consider populations to be clonal. The term *community* refers to the collection of all resident populations.

We will denote a resident's strategy as X and an invader's as Y. Hence a community with N different strategies present, would consist of the types $1, 2, \ldots$ to N, distinguished by their stategies $X_1, X_2, \ldots$ to X_N. The community as a whole is indicated by $\mathbb{X} := \{X_1, X_2, \ldots, X_N\}$.

The invasion fitness function as defined above will be referred to as the s-function; this choice of notation underlines its heritage as a conceptual extension of the selection coefficient of population genetics. A *monomorphic s-function* $s_X(Y)$ describes the invasion fitness of a mutant with type Y in an environment set by a population of X-type residents. In the case of a community of N populations, we similarly speak of a *polymorphic s-function* and denote it by $s_{X_1, X_2, \ldots, X_N}(Y)$ to show which N strategies are present.

A further set of functions of central concern are the *invasion gradients*. The invasion gradient at a given strategy X_i is the derivative of s in the mutant

direction at that trait value: $\frac{\partial s_{\mathbb{X}}(\boldsymbol{Y})}{\partial \boldsymbol{Y}}\big|_{\boldsymbol{Y}=\boldsymbol{X}_i}$. Trait values where the invasion gradient is zero, are called *evolutionary singular strategies*; they are particularly interesting as they are possible evolutionary endpoints (attracting, noninvadable points), or sources of diversity (branching points).

For mathematical reasons, the existence of a unique, fixed-point attractor for the community as a whole is usually assumed. We restrict ourselves in this section to attractors composed of positive equilibrium densities for the N types that make up the community. The basic assumption of rare mutations implies that between two mutation events the population dynamics has settled at its attractor. So in an N-species community at equilibrium where there is a mutation in the ith species, a mutant $\boldsymbol{Y} \approx \boldsymbol{X}_i$ will be introduced. After some time, the community will again have reached an equilibrium state. Which N stategies will make up this new attractor, depends on whether the mutant has disappeared or driven its ancestor to extinction: we deal in this section only with situations away from singularities, so that "invasion implies fixation" holds.

Time will always be scaled such that it reflects slow, evolutionary time and not the much faster, ecological time scale. Then the population dynamics will be so rapid that the community always seems to be at its attractor, at densities determined by the unique equilibrium for the set of strategies present. This way, the N strategies present will indeed fully describe the community at each point in time.

3 The deterministic path

The canonical equation is a first-order prediction for the speed of trait evolution. This estimate of the rate at which strategy substitutions happen is valid under a regime of directional selection; that is to say, away from evolutionary singular strategies, so that the fitness gradient $\frac{\partial s_{\boldsymbol{X}_1, \boldsymbol{X}_2, \dots, \boldsymbol{X}_N}(\boldsymbol{Y})}{\partial \boldsymbol{Y}}$ is nonzero.

As put forward in the assumptions, the resident community is very large and hence can be described by a deterministic model. Furthermore we can regard the population dynamics as stationary, due to the assumption that it has a fixed-point attractor. However, the appearance of mutants and their eventual success or failure at establishment both are inherently stochastic processes. This makes the trait values themselves stochastic and time-dependent. As we are dealing with a Markov process, the community has a probability $\Pi(\mathbb{X}, t)$ of being in state $\mathbb{X}$ at time $t > 0$. This probability can be calculated from the state at $t = 0$ together with all transition rates $\pi(B, A)$ from state A into B.

Since we consider rare mutations, any transition must be a mutation affecting a single strategy vector, simplifying $\pi(A, B)$: all the action will come from terms $\pi_0(\boldsymbol{X}'_i, \boldsymbol{X}_i, \mathbb{X})$, which are the rates at which the ith species (known by its strategy $\boldsymbol{X}_i$) in community $\mathbb{X}$ is replaced by one with strategy $\boldsymbol{X}'_i$.

Application of the Kolmogorov backwards equations to the right hand side of $\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}\left[\mathbb{X}\right] := \int \mathbb{X}\frac{\partial \Pi(\mathbb{X},t)}{\partial t}\,\mathrm{d}\mathbb{X}$ will show after some algebra that the expected rate of evolutionary change is

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}[\mathbb{X}] = \mathbb{E}[\mathsf{J}(\mathbb{X})] \tag{1}$$

where $\mathsf{J}(\mathbb{X})$ is an N-by-N matrix with i^{th} column $\int (\boldsymbol{X}' - \boldsymbol{X}_i)\pi_0(\boldsymbol{X}', \boldsymbol{X}_i, \mathbb{X})\,\mathrm{d}\boldsymbol{X}'$. The unique solution satisfying a given initial condition is called the *mean path* starting from that given state. If J happens to be a linear function of $\mathbb{X}$, or if the distribution of $\mathbb{X}$ is concentrated in a point, we would have the following, self-contained equation:

$$\tfrac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}[\mathbb{X}] = \mathsf{J}(\mathbb{E}[\mathbb{X}]) \qquad (2)$$

The solution to this simplified problem is called the *deterministic path*. The validity of this approximation has been argued, based on considerations in van Kampen (1981) as well as simulations, in Dieckmann and Law (1996). It hinges on whether the solution to Equation (1) is dominated by the first-order part of the equation or not. One can intuitively expect this to happen, as the path proceeds in time by very many very small steps. Then some effect similar to the law-of-large-numbers leads to a concentrated distribution of $\mathbb{X}$ and hence to the applicability of the approximation (2). This heuristic idea is explored in a mathematically rigorous fashion in Champagnat *et al.* (2001), based on convergence theorems in Ethier and Kurtz (1986).

We will follow the assumption that a deterministic approximation is valid, and henceforward focus on the attendant path. To lighten the notation, we write $\boldsymbol{X}_i$ instead of $\mathbb{E}[\boldsymbol{X}_i]$ for each resident and similar for $\mathbb{X}$ as they will all be expected values from here onwards (not so for invaders $\boldsymbol{Y}$ or mutants $\boldsymbol{X}'_i$). Our concrete aim is then to derive analytical expressions for the right hand side of

$$\frac{\mathrm{d}}{\mathrm{d}t}\boldsymbol{X}_i \;\; = \;\; \int (\boldsymbol{X}' - \boldsymbol{X}_i)\pi_0(\boldsymbol{X}', \boldsymbol{X}_i, \mathbb{X})\,\mathrm{d}\boldsymbol{X}' \qquad (3)$$

for all species i in the community. The first step is to separate the factors that make up the transition probability π_0. Seeing that mutation and selection are independent processes, it must be the product of the appearance rate of mutants with their establishment probability:

$$
\begin{aligned}
&\pi_0(\boldsymbol{X}'_i, \boldsymbol{X}_i, \mathbb{X}) \\
&\quad = \;\; (\text{rate of mutations } \boldsymbol{X}_i \to \boldsymbol{X}'_i \text{ given } \mathbb{X})\,(\text{establishment chance}) \\
&\quad = \;\; \overbrace{(\text{birth rate of } \boldsymbol{X}_i \text{ types})}\;\overbrace{(\text{mutation chance } \boldsymbol{X}_i \to \boldsymbol{X}'_i)}\;\overbrace{P(\boldsymbol{X}'_i, \mathbb{X})} \\
&\quad = \;\; \overbrace{\lambda(\boldsymbol{X}_i, \mathbb{X})\quad \hat{n}_i}\qquad \overbrace{\mu(\boldsymbol{X}_i)\quad \mathfrak{M}(\boldsymbol{X}'_i - \boldsymbol{X}_i, \boldsymbol{X}_i)}\quad P(\boldsymbol{X}'_i, \mathbb{X}) \quad (4)
\end{aligned}
$$

At this point we stress that above we are treating expected values, but simplified the notation; $\hat{n}_i$ denotes the equilibrium density of the ith species.

The chance P of establishment warrants a separate computation, but the other factors are intuitive. The verbal reasoning is that the production rate of mutants descending from a $\boldsymbol{X}_i$-type parent is just the total production of $\boldsymbol{X}_i$-type offspring, times the mutation chance. The production rate of $\boldsymbol{X}_i$ strategists is the per capita birth rate λ times the equilibrium density $\hat{n}_i \equiv \hat{n}(\boldsymbol{X}_i; \boldsymbol{X}_1, \boldsymbol{X}_2, \ldots, \boldsymbol{X}_N)$ in the given community. Which and how many mutants appear (as a fraction of the newborns), is the product of the mutation probability μ per birth event with the mutational distribution $\mathfrak{M}(\boldsymbol{V}, \boldsymbol{X}_i)$, i.e. the probability that the mutation changes a trait value from $\boldsymbol{X}_i$ to $\boldsymbol{X}_i + \boldsymbol{V}$.

Under very general conditions, the per capita birth rate in a closed, critical system is the inverse of the expected lifespan. The argumentation has been called the *microcosm principle* by Mollison (1995) and goes as follows: in a large population ergodically fluctuating around its attracting density,

$$
\begin{aligned}
\mathbb{E}[\text{density}] &= \mathbb{E}[\text{influx of individuals per area}] \, \mathbb{E}[\text{duration of stay}] \\
&= \mathbb{E}[\text{per capita birth rate}] \, \mathbb{E}[\text{density}] \, \mathbb{E}[\text{life span}] \\
\hat{n}_i &= \lambda(\boldsymbol{X}_i, \mathbb{X}) \, \hat{n}_i \, \mathbb{E}[\text{life span}]
\end{aligned}
$$

Hence the life expectancy

$$
T \equiv T(\boldsymbol{X}_i, \mathbb{X}) = \lambda^{-1}(\boldsymbol{X}_i, \mathbb{X}) \tag{5}
$$

for any resident. This assumes closed populations, so that influx is only caused by reproduction, and an individual's stay is only ended by death.

The chance of establishment P depends on the underlying population model. As presented by Dieckmann and Law (1996), the canonical equation tradionally considers unstructured populations in continuous time. In that case, a linear birth-and-death process determines the fate of the mutants. We will however allow populations structured e.g. by size, or by sexual differences. For that, we introduce the concepts of structured population models as far as needed to estimate P.

4 Physiologically structured population models

We want to consider as wide as possible a variety of models to which our calculations apply. The two best-known classes of demographic models are probably Lotka-Volterra and stage- (or age-) structured matrix models. Both have their shortcomings: matrix models can only deal with finite numbers of discrete stages, and time must be discrete too. In Lotka-Volterra models all individuals are born equal and their death rates are independent of age or reproductive state. The whole population is essentially a soup of identical creatures.

We therefore consider the class of physiologically structured population models, which has both Lotka-Volterra and matrix models as subclasses. Section 4.3 gives a more detailed, mathematical description of this class, but the biological considerations that shape the formalism are

size does matter A large fish may happily eat a smaller conspecific, but will refrain from attacking a similar-sized, healthy individual; a nice fat insect will lay more eggs, and a big baby has a head start in life.

Furthermore, reaching a given size may trigger a stage-transition. A look at a life cycle diagram for any insect will convince you that these are important events. Thinking further along these lines, this life cycle may depend equally drastic on the sex of the individual or similar characteristics. Populations could also live on several patches where resource availability differs.

All these features together form the *states* an individual can be in, whether they are described as continuous (like size or age), or discrete (like stage or sex). We will try to convince you later on that we can focus on only the *birth states*, those states that individuals possibly start their life in. Examples could be the size of a plant seed, the mass of the yolk in an egg, the gender or morph of an individual.

conditional linearity A key insight to disentangle the interactions between individuals in a community, is the *separation of individual and environment*. One has to conceive of a formal environment that influences individuals and vice versa through a feedback loop. The implicit definition is that given an environment, all individuals are independent.

The environmental condition must contain all information to predict what will happen the next moment to each individual. In other words: given the environment, an individual's fate is a Markov process (Section 2.5). The feedback loop is closed by the simple fact, that each individual is accounted for when calculating the condition of the environment. The reader is referred to the discussion in Sections 2.9 and 5.10 to relate this concept of environment to the view in branching processes.

For example, if gender matters and competition acts differently within age classes than across, then the environment will have components showing densities and sex ratios in each class separately. Furthermore, the environment will logically also have components describing relevant external parameters that may have their own dynamics, like temperature, influx of resources, or harvesting.

The idea that such an environment can be constructed is justified in large populations: any two individuals, being exceedingly rare as a proportion of the total population, will experience the same world populated by the same types, states and quantities of 'others' even if their expected reaction to it may differ, depending on personal state and strategy. This decoupling of individual and environment is a helpful step in the systematic understanding of structured population models (see Metz and Diekmann 1986, Diekmann *et al.* 2003) and linearizes the equations when the environment is given as a function of time. Deriving the correct description of the environment may cost a lot of work in specific situations, but most models are presented in a way that the derivation is trivial.

At this point, it is important to distinguish strategies and birth states: both are parameters an individual starts its life with, and some states like sex might never change in one's lifetime. One requires a priori that the life history of all individuals with a given strategy can be sketched in one indecomposable life cycle graph. If not, there would be isolated groups that can be separated into species by adding a parameter to the strategy. This consideration provides a strict distinction between traits and birth states in models where individuals with different strategies cannot reproduce together, which we have trivially guaranteed by assuming clonal reproduction. An intuitive example of the dis-

tinction between strategy and birth state is seed size in plants (Geritz *et al.* 1999). Part of a plant's strategy may be the decision to allocate its energy reserve into many small seeds with a low survival chance, few large seeds with a good chance, or a given mixture of these; while a plant's birth state can be the size it has as a seed.

That birth states suffice to study invasion demographics follows from uncoupling the feedback loop. If one assumes that the environment is constant, one can calculate for any given newborn the probability of being in each possible state at each later moment. Similarly for an individual in a given state, the chance of having any amount of newborns in any birth state can be computed for any later point in time. By combining these, one finds for any given newborn the environment-dependent probabilities of having any amount of offspring in any birth state at any later moment. From this generational viewpoint, birth states are the only thing to keep track of. This is an important observation that forms the basis of multi-type branching processes. Furthermore, for a deterministic population being at equilibrium must mean that in each generation there are born an exact quantity of young in each birth state, such that the individuals have on average precisely one offspring over their lifetime, and the new generation has the same distribution of birth states as the former. Note that this applies whether time is discrete or continuous in the underlying model. In short, only lifetime offspring production from individuals starting in birth states are what counts.

We will denote by $\boldsymbol{I} \equiv \boldsymbol{I}(\boldsymbol{X}_1, \boldsymbol{X}_2, \ldots, \boldsymbol{X}_N)$ the environment as set by the resident community and consider a given invader with strategy $\boldsymbol{Y}$. For any structured population model, there must necessarily exist a *reproduction kernel* which we formulate here as a matrix function with entries $(\Lambda(\boldsymbol{Y}, \boldsymbol{I}, a))_{hj}$ that are the expected number of $\boldsymbol{Y}$-type invaders born in state j to an invader newly born in state h, before it reaches age a if the environment is in state $\boldsymbol{I}$. Here we remark that $\Lambda(\boldsymbol{Y}, \boldsymbol{I}, \mathrm{d}a)$ corresponds to $\mu(r, ds \times da)$ as introduced in Section 3.3, and that the connection to the mean matrix is seen from

$$\mathbb{E}[\xi_{hj}] = \Lambda(\boldsymbol{Y}, \boldsymbol{I}, \infty)_{hj}$$

where the strategy and environment must be the same on both sides of the equality. We conform here to branching processes notation, insofar that Λ is usually defined as its transpose in structured populations literature.

According to the definition we gave, the (generally unique) solution for ψ of Lotka's equation

$$\text{Dominant Eigenvalue of } \left[\int_0^\infty e^{-\psi a} \Lambda(\boldsymbol{Y}, \boldsymbol{I}, \mathrm{d}a) \right] = 1$$

is the invasion fitness $\boldsymbol{s}_{\boldsymbol{X}_1, \boldsymbol{X}_2, \ldots, \boldsymbol{X}_N}(\boldsymbol{Y})$. Alternatively, it is called the instantaneous growth rate r in life history theory, or the Malthusian parameter α in branching processes.

If one fixes $\psi = 0$, the integral on the left hand side corresponds to the mean matrix as used throughout this book, and its dominant eigenvalue is the

lifetime reproductive output R_0 which is denoted by ρ in branching processes. The notation R_0 is also the traditional notation in life history theory as well as in epidemiology, where it is the expected number of secondary infections caused by an infective individual (see the snappily titled thesis of Hans Heesterbeek 1992).

Durinx *et al.* (in prep.) show by a Taylor expansion of the left hand side around $\psi = 0$ that for any mutant $\boldsymbol{Y}$, we have the relationship

$$\boldsymbol{s}_{\mathbb{X}}(\boldsymbol{Y}) = \frac{\ln R_0}{\beta(0)} + o(\ln R_0) \tag{6}$$

where the *average age at giving birth* $\beta(0)$ is that of the mutant's progenitor, calculated from the reproduction kernel as

$$\beta(0) \equiv \beta(\boldsymbol{X}_i, I) = \boldsymbol{u}(0)^{\mathsf{T}} \left[\int_0^\infty a\Lambda(\boldsymbol{X}_i, \boldsymbol{I}, \mathrm{d}a) \right] \boldsymbol{v}(0)$$

with $\boldsymbol{u}(0)$ the 'stable type distribution' of the resident, which in our context is its *stable birth state distribution*, and $\boldsymbol{v}(0)$ its reproductive value.

5 The establishment probability

The first paragraph on invasion fitness verbally stated that under very general conditions, a positive chance of establishment is equivalent to a positive $\boldsymbol{s}$-value:

$$P(\boldsymbol{Y}, \mathbb{X}) > 0 \Leftrightarrow \boldsymbol{s}_{\mathbb{X}}(\boldsymbol{Y}) > 0$$

We must now seek a more quantitative relationship between these terms.

Consider that we have been given an invader that differs but slightly from one of the resident species; each of these types has zero growth rate in the community as we assumed it to be stationary. Hence the d-type branching process that describes the fate of this mutant is slightly supercritical: $R_0 = 1 + \varepsilon$ for a small $\varepsilon > 0$. As explained in Section 5.6, Athreya (1993) proved that under very general conditions, the establishment probability of a single mutant with birth state h can therefore be approximated by

$$P_h(\boldsymbol{X}_i', \mathbb{X}) = 2\frac{R_0 - 1}{B(\varepsilon)}\boldsymbol{v}(\varepsilon)_h + o(\varepsilon) = 2\frac{\ln R_0}{B(\varepsilon)}\boldsymbol{v}(\varepsilon)_h + o(\varepsilon)$$

where $\boldsymbol{v}(\varepsilon)$ denotes the mutant's reproductive value. This complies with our earlier notation as the ith resident naturally has $\varepsilon = 0$, and the same applies to the parameters $\boldsymbol{u}(\varepsilon)$ and $\xi(\varepsilon)_{hj}$. The factor $B(\varepsilon)$ may be interpreted as a variance (see Durinx *et al.* (in prep.)):

$$B(\varepsilon) = \sum_j \boldsymbol{u}(\varepsilon)_j \mathrm{Var}[\sum_l \boldsymbol{v}(\varepsilon)_l \xi(\varepsilon)_{lj}] + o(1)$$

The initial mutant has probability $\boldsymbol{u}(0)_h$ of being born in state h, since $\boldsymbol{u}(0)$ is the stationary offspring distribution of its parent. As the eigenvectors for

9

residents and mutants differ at most by order ε, we can here approximate $\boldsymbol{v}(\varepsilon)_h$ by $\boldsymbol{v}(0)_h$ and so forth, showing that

$$
\begin{aligned}
P(\boldsymbol{X}_i', \mathbb{X}) &= \sum_h \boldsymbol{u}(0)_h P_h(\boldsymbol{X}_i', \mathbb{X}) \\
&= 2 \sum_h \boldsymbol{u}(0)_h \boldsymbol{v}(0)_h \frac{\ln R_0}{\sum_j \boldsymbol{u}(0)_j \mathrm{Var}[\sum_l \boldsymbol{v}(0)_l \xi(0)_{lj}]} + o(\varepsilon) \\
&= \frac{2 \ln R_0}{\sum_j \boldsymbol{u}(0)_j \mathrm{Var}[\sum_l \boldsymbol{v}(0)_l \xi(0)_{lj}]} + o(\varepsilon)
\end{aligned}
$$

since the product of the eigenvectors sums to one (see Section 2.3).

This means we can wrap up the formulation of the establishment probability by substituting the relation (6) we found between $\boldsymbol{s}$ and R_0 and finally by linearly approximating $\boldsymbol{s}_{\mathbb{X}}(\boldsymbol{X}_i')$ close to $\boldsymbol{s}_{\mathbb{X}}(\boldsymbol{X}_i) = 0$:

$$
\begin{aligned}
P(\boldsymbol{X}_i', \mathbb{X}) &= \frac{2\beta(0)\, \boldsymbol{s}_{\mathbb{X}}(\boldsymbol{X}_i')}{\sum_j \boldsymbol{u}(0)_j \mathrm{Var}[\sum_l \boldsymbol{v}(0)_l \xi(0)_{lj}]} + o(\varepsilon) && (7) \\
&= \frac{2\beta(0)}{\sum_j \boldsymbol{u}(0)_j \mathrm{Var}[\sum_l \boldsymbol{v}(0)_l \xi(0)_{lj}]} (\boldsymbol{X}_i' - \boldsymbol{X}_i)^{\mathsf{T}} \frac{\partial S_{\mathbb{X}}(\boldsymbol{X}_i)^{\mathsf{T}}}{\partial \boldsymbol{Y}} + o(\varepsilon) && (8)
\end{aligned}
$$

Note that we use values derived for $\boldsymbol{X}_i$ for all but the mutation step $(\boldsymbol{X}_i' - \boldsymbol{X}_i)$.

More importantly, bear in mind that the above approximation only holds if it returns a positive value, as we started by assuming $\varepsilon > 0$.

6   The canonical equation for structured populations

The calculated transition rates (4) combined with the microcosm principle (5) and the estimated chance of establishment (8), show that the evolutionary movement along deterministic path (3) is generated by

$$
\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t} \boldsymbol{X}_i &= \int (\boldsymbol{X}_i' - \boldsymbol{X}_i) \frac{\hat{n}_i \mu(\boldsymbol{X}_i)}{T} \mathfrak{M}(\boldsymbol{X}_i' - \boldsymbol{X}_i, \boldsymbol{X}_i) P(\boldsymbol{X}_i', \mathbb{X})\, \mathrm{d}\boldsymbol{X}_i' \\
&= \frac{\beta\, \hat{n}_i\, \mu(\boldsymbol{X}_i)}{T \sum_j \boldsymbol{u}_j \mathrm{Var}[\sum_l \boldsymbol{v}_l \xi_{lj}]} \int \boldsymbol{V} \mathfrak{M}(\boldsymbol{V}, \boldsymbol{X}_i) \boldsymbol{V}^{\mathsf{T}} \frac{\partial S_{\mathbb{X}}(\boldsymbol{X}_i)^{\mathsf{T}}}{\partial \boldsymbol{Y}}\, \mathrm{d}\boldsymbol{V} + o(\varepsilon) \\
&= \frac{\beta\, \hat{n}_i\, \mu(\boldsymbol{X}_i)}{T \sum_j \boldsymbol{u}_j \mathrm{Var}[\sum_l \boldsymbol{v}_l \xi_{lj}]} \mathbb{M}(\boldsymbol{X}_i) \frac{\partial S_{\mathbb{X}}(\boldsymbol{X}_i)^{\mathsf{T}}}{\partial \boldsymbol{Y}} + o(\varepsilon)
\end{aligned}
$$

with $\mathbb{M}(\boldsymbol{X}_i) := \int \boldsymbol{V} \mathfrak{M}(\boldsymbol{V}, \boldsymbol{X}_i) \boldsymbol{V}^{\mathsf{T}}\, \mathrm{d}\boldsymbol{V}$ the *mutational covariance matrix at $\boldsymbol{X}_i$*.

The second remark after (8) explains the disappearance of the factor 2 in the first equality above: for each strategy $\boldsymbol{V}$ that returns a positive value for $\boldsymbol{V}^{\mathsf{T}} \frac{\partial S_{\mathbb{X}}(\boldsymbol{X}_i)^{\mathsf{T}}}{\partial \boldsymbol{Y}}$, the strategy $-\boldsymbol{V}$ returns a negative value, and vice versa since we are away from singular strategies. Hence we have to replace exactly half of the

estimates by zero. The value under the integral is not influenced by this, as $\boldsymbol{V}$ and $-\boldsymbol{V}$ return the same value under the second integral if the distribution $\mathfrak{M}$ is symmetrical.

This lets us finalize the canonical equation for structured populations as the first order prediction

$$\frac{\mathrm{d}}{\mathrm{d}t}\boldsymbol{X}_i \approx \frac{\beta}{T}\frac{\hat{n}_i\,\mu(\boldsymbol{X}_i)}{\sum_j \boldsymbol{u}_j \mathrm{Var}[\sum_l \boldsymbol{v}_l \xi_{lj}]}\mathbb{M}(\boldsymbol{X}_i)\frac{\partial S_{\mathbb{X}}(\boldsymbol{X}_i)}{\partial \boldsymbol{Y}}^{\mathsf{T}}$$

It should be kept in mind that these are all expected values for each of the parameters and strategies, and that most parameters relating to a species i depend on the other strategies in the community $\mathbb{X}$ as well.

7 Discussion

A fundamental open problem in evolutionary biology is the development of a straightforward, systematic way to study long-term evolutionary trajectories. Over the years, some of the issues have been adressed.

How selection can change morphological traits was first described by Lande (1979) based on the breeder's equation as found in animal sciences. In what has become known in evolutionary biology as Lande's equation, we see a formula that is remarkably similar to the canonical equation. The major difference is that the population density does not appear as a factor, the other differences amount to a different interpretation of the parameters. What it essentially describes is how a population changes through selection on standing genetic variation. Such variation accumulates when a species' strategy is close to evolutionarily optimal in a stable environment, especially if the optimum is relatively weak. Selection on the diversity then occurs when external environmental parameters change. A typical example of this is the introduction of a wild population into a laboratory setup where directional selection is applied, accounting for the good fit of Lande's equation with lab data. After the initial relatively rapid modification of the traits in reaction to external changes, further innovations and long-term evolution must come from mutations. Haldane (1927) was the first to realize this and to argue that mutation limited evolution will be slower than one would initially suspect, since many advantageous mutants will fail to get established. The canonical equation builds on those ideas to derive a quantitative relation between the factors involved and in particular how the ecology determines the selective pressures.

It is clear that the assumptions we have worked with amount to a crude oversimplification, but the question is important: how can we link ecology with paleontology? The Modern Synthesis went no further than showing that the two are compatible. Lande's equation and the canonical equation are the best (being the only) tools we have so far for reasoning about the connection.

This section illustrates how branching processes underlie mutation limited evolution and hence their fundamental importance to adaptive dynamics theory.

The calculations were meant to be heuristic and biological, at a cost to mathematical precision and exhaustiveness. For a more mathematical treatment of the canonical equation one can consult Champagnat *et al.* (2001). The restriction to finitely many possible birth states means we can fall back on established theory, but limits the applicability. To overcome this requires an extension of the theorem of Section 5.6.2 (Athreya 1993) to branching processes with infinitely many types. If the resident attractor is not a fixed point but a limit cycle, every individual can be assigned a birth state that depends on where in the cycle the individual was born. In discrete time this allows the attractor to be treated analogous to a fixed point, so that our analysis immediately applies. In continuous time the suggested extension of Athreya's proof would be similarly applied.

Analytically there is no extension of the canonical equation to nonperiodic attractors yet. The first heuristic explorations for ergodically fluctuating environments with invader dynamics that follow a linear birth-and-death process, suggest that the canonical equation is robust against such extension. Dieckmann (in prep.) shows by approximating the process as formulated in Kendall (1948), that the establishment probability is approximately proportional to the fitness (as in Equation 7), so that a similar result holds.

The analysis as presented applies to spatial models with finite numbers of patches, if the residents are locally sufficiently numerous and well-mixed. The patch an individual inhabits is then expressed in a component of its state. For some more complicated spatial models an equation similar to the canonical equation may well apply. The crucial part is that the chance of success at invading must scale linearly with changes in strategy. This is an area where more research is badly needed.

We did assume an unbiased mutation distribution. Mutation bias arises from the nonlinearity of the genotype-phenotype mapping, and becomes prominent when high mutational variance is combined with a highly curved mapping. However, since we assume small mutational steps, we follow the biological literature in neglecting this effect. Champagnat *et al.* (2001) discusses the relevance of bias in the context of the canonical equation.

A far more complicated issue is the one underlying time scale separation. There are several latent limits: large resident populations (or the limit $\frac{1}{\Omega} \to 0$ where Ω is the system size), small mutations (or $\epsilon \to 0$) and rare mutations (or $\mu(\boldsymbol{X}_i)\Omega \to 0$). These limits are not a priori commutative, so depending on the order in which the details of mechanistic, individual based parameters are scaled away, a different limit process is obtained. An initial discussion of these issues, in particular of the necessity to stay away from singularities, can be found in Metz *et al.* (1996).

8 Acknowledgements

9   References

1. Athreya, K.B.: Rates of decay for the survival probability of a mutant gene II The multitype case. J. Math. Biol. **32** 45–93 (1993)

2. Champagnat, N., Ferrière, R., Arous, G.B.: The canonical equation of adaptive dynamics: a mathematical view. Selection **2** 73-83 (2001)

3. Dieckmann, U., Doebeli, M., Metz, J.A.J., Tautz, D.: *Adaptive Speciation.* Cambridge studies in adaptive dynamics 3. Cambridge U. Press (2004)

4. Dieckmann, U., Law, R.: The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. **34** 579–612 (1996)

5. Diekmann, O., Gyllenberg, M., Metz, J.A.J.: Steady state analysis of structured population models. Theor. Pop. Biol. **63** 309–338 (2003)

6. Ethier, S.N., Kurtz, T.G.: *Markov Processes, Characterization and Convergence.* J. Wiley and Sons (1986)

7. Geritz, S.A.H., van der Meijden, E., Metz, J.A.J.: Evolutionary dynamics of seed size and seedling competitive ability. Theor. Pop. Biol. **55 (3)** 324–343 (1999)

8. Geritz, S.A.H., Gyllenberg, M., Jacobs, F.J.A., Parvinen, K.: Invasion dynamics and attractor inheritance. J. Math. Biol. **44** 548–560 (2002)

9. Gyllenberg, M., Parvinen, K.: Necessary and sufficient conditions for evolutionary suicide. Bull. Math. biol. **63 (5)** 981–993 (2001)

10. Haldane, J.B.S.: A mathematical theory of natural and artificial selection. V: Selection and mutation. Proc. Camb. Phil. Soc. **23** 838–844 (1927)

11. Heesterbeek Heesterbeek, H.: R_0. PhD thesis, Leiden University (1992)

12. Kendall, D.G.: On the generalized "birth-and-death" process. Ann. Math. Statist. **19** 1–15 (1948)

13. Lande, R.: Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evolution **33** 402–416 (1979)

14. Maynard Smith, J.: *Evolution and the Theory of Games.* Cambridge University Press (1982)

15. Metz, J.A.J., Diekmann, O. eds. *The Dynamics of Physiologically Structured Populations.* Lecture Notes in Biomathematics 68. Springer Verlag (1986)

16. Metz, J.A.J., Geritz, S.A.H., Meszena, G., Jacobs, F.J.A., Van Heerwaarden, J.S.: Adaptive Dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems*, Van Strien, S.J., Verduyn Lunel, S.M. editors, North-Holland (1996)

17. Mollison, D.: The structure of epidemic models. In Mollison, D. ed. *Epidemic Models, their Structure and Relation to Data.* Cambridge U. Press (1995)

18. van Kampen, N.G.: *Stochastic Processes in Physics and Chemistry.* North Holland (1981)