

The hitchhiker's guide to Adaptive Dynamics

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1. Introduction

The basic principle of evolution, survival of the fittest*, was outlined by the naturalist Charles Darwin in his 1859 book *On the origin of species*. Though controversial at the time, the central ideas remain virtually unchanged to this date, even though much more is now known about the biological basis of inheritance. Darwin expressed his arguments verbally, but many attempts have since then been made to formalise the theory of evolution. The perhaps most well known are population genetics (Roughgarden, 1979) which aim to model the biological basis of inheritance but usually at the expense of ecological detail, quantitative genetics (Falconer & Mackay, 1996) which incorporates quantitative traits influenced by genes at many loci and evolutionary game theory (Hofbauer & Sigmund, 1998) which ignores genetic detail but incorporates a high degree of ecological realism, in particular that the success of any given strategy depends on the frequency at which strategies are played in the population, a concept known as *frequency dependence*.

Adaptive Dynamics is a set of techniques developed during the 1990s for understanding the long-term consequences of small mutations in the traits expressing the phenotype. They link *population dynamics* to evolutionary dynamics and incorporate and generalises the fundamental idea of frequency dependent selection from game theory. The number of papers using Adaptive Dynamics techniques is increasing steadily as Adaptive Dynamics is gaining ground as a versatile tool for evolutionary modelling. This manuscript is aimed at researchers and students wanting to learn Adaptive Dynamics to the level necessary to follow the arguments made in these papers.

In the next section we introduce the fundamental ideas behind Adaptive Dynamics. Then, in Section 3, the theory is presented in detail for *monomorphic* populations. In particular, we will explain the *invasion exponent*, *pairwise-invasibility plots*, the *selec-*

*To be precise, the phrase 'survival of the fittest' was coined by the philosopher Herbert Spencer and adopted by Darwin from the fifth edition of *On the origin of species*

tion gradient, *Evolutionarily Singular Strategies* and the *canonical equation*. Section 4 extends these concepts to *polymorphic* populations and introduces *trait evolution plots*. Finally we conclude with a discussion of the applicability and limitations of the Adaptive Dynamics' techniques presented here.

2. Fundamental ideas

Two fundamental ideas of Adaptive Dynamics are that the resident population can be assumed to be in a dynamical equilibrium when new mutants appear, and that the eventual fate of such mutants can be inferred from their initial growth rate when rare in the environment consisting of the resident. This rate is known as the invasion exponent when measured as the initial exponential growth rate of mutants (Diekmann, 2003), and as the *basic reproductive number* when it measures the expected total number of offspring that a mutant individual will produce in a life time. It can be thought of and is indeed sometimes also referred to as invasion fitness of mutants. In order to make use of these ideas we require a mathematical model that explicitly incorporates the traits undergoing evolutionary change. The model should describe both the environment and the population dynamics given the environment, but in many cases the variable part of the environment consist only of the demography of the current population. We then determine the invasion exponent, the initial growth rate of a mutant invading the environment consisting of the resident. Depending on the model, this can be trivial or very difficult, but once determined the Adaptive Dynamics techniques can be applied independent of the model structure. In the next section we will introduce the basic theory for monomorphic populations.

3. Monomorphic evolution

A population consisting of individuals with the same trait is called monomorphic. If not explicitly stated differently we will assume that the trait is a real number and we will write r and m for the trait value of the monomorphic resident population and that of an invading mutant respectively.

3.1. Invasion exponent and selection gradient

The invasion exponent $S_r(m)$ is defined as the expected growth rate of an initially rare mutant in the environment set by the resident, which simply means the frequency of each phenotype (trait value) whenever this suffices to infer all other aspects of the equilibrium environment, such as the demographic composition and the availability of resources. For each r the invasion exponent can be thought of as the fitness landscape experienced by an initially rare mutant. The landscape changes with each successful invasion (see Figure 1) as is the case in evolutionary game theory, but in contrast with the classical view of evolution as an optimisation process towards ever higher fitness. We will always assume that the resident is at its demographic attractor, and as a consequence $S_r(r) = 0$ for all r as otherwise the population would grow indefinitely.

The selection gradient is defined as the slope of the invasion exponent at $m = r$ (see

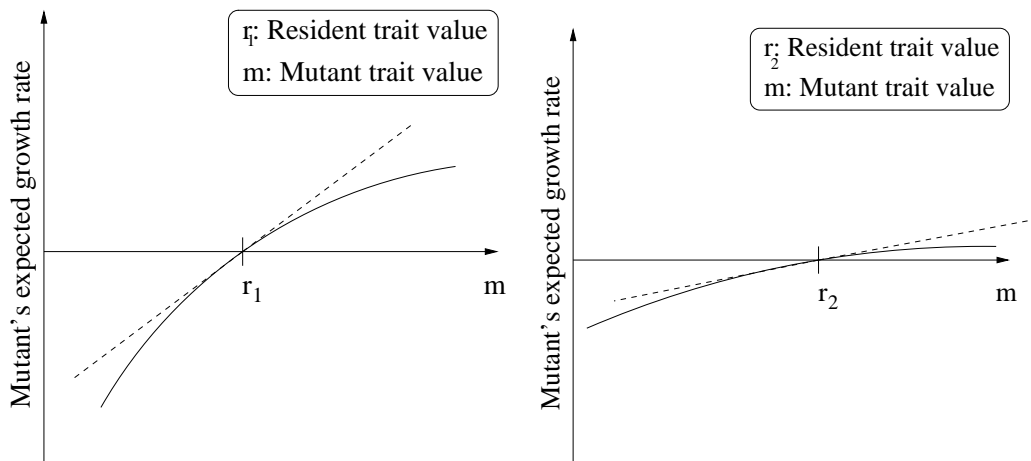


Figure 1: Plot of the invasion exponent $S_r(m)$, the expected growth rate of a rare mutant in the environment set by the resident (solid lines), as a function of the mutant trait value m , for two illustrative cases. The dashed lines denote the local tangent of $S_r(m)$ at $m = r$ where its slope corresponds to the selection gradient $S'_r(r)$. a) The population is monomorphic and consists of only the phenotypes corresponding to trait value r_1 . Mutants with higher trait values have positive expected growth rate and can hence invade. b) A mutant with trait value r_2 has invaded and successfully replaced the resident. Since the population now consists of a new phenotype, namely that corresponding to trait value r_2 , the fitness landscape itself has changed. Note that the invasion exponent vanishes exactly when the mutant trait equals that of the resident, $m = r$.

Figure 1), $S'_r(r)$. If the sign of the invasion exponent is positive (negative) mutants with slightly higher (lower) trait values may successfully invade. This follows from the linear approximation $S_r(m) \approx S'_r(r)(m - r)$, which holds whenever $m \approx r$.

3.2. Pairwise-invasibility plots

The invasion exponent represents the fitness landscape as experienced by a rare mutant. In a large (infinite) population only mutants with trait values m for which $S_r(m)$ is positive are able to successfully invade. The generic outcome of an invasion is that the mutant replaces the resident, and the fitness landscape as experienced by a rare mutant changes. To determine the outcome of the resulting series of invasions pairwise-invasibility plots (PIPs) are often used. These show for each resident trait value r all mutant trait values m for which $S_r(m)$ is positive. Three examples are given in figure 2. The grey area marked with '+' corresponds to pairs r and m for which a mutant with trait value m can successfully invade a resident population with trait value r , i.e. $S_r(m) > 0$. Note that $S_r(m)$ is zero at the diagonal $m = r$. In PIPs the fitness landscapes as experienced by a rare mutant (see Fig. 1) correspond to the vertical lines where the resident trait value r is constant.

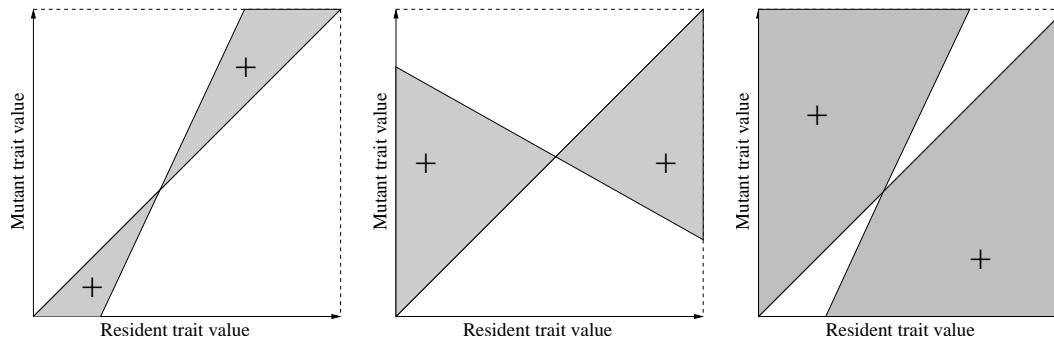


Figure 2: Examples of pairwise invasibility plots. Gray shading denotes positive invader growth rate $S_r(m)$, white shading negative $S_r(m)$, the black diagonal lines $S_r(m) = 0$. a) Evolutionarily stable strategy but not convergence stable. Such strategies should be rare in nature: if the strategy is once established it cannot be invaded locally, but it cannot be approached gradually in small steps, either. b) Evolutionarily stable strategy and convergence stable. A possible endpoint of evolution: the strategy can be attained gradually and then it will resist any invaders successfully. c) Convergence stable strategy but not evolutionarily stable. A scenario where a population can become dimorphic: the singular strategy can be established gradually, but then it can be invaded by mutants both above and below the resident strategy at the same time.

3.3. Evolutionarily singular strategies

The selection gradient $S'_r(r)$ determines the direction of evolutionary change. If it is positive (negative) a mutant with a slightly higher (lower) trait-value will generically invade and replace the resident. But what will happen if $S'_r(r)$ vanishes? Seemingly evolution should come to a halt at such a point. While this is a possible outcome, the general situation is more complex. Traits or strategies r^* for which $S'_{r^*}(r^*) = 0$, are known as *evolutionarily singular strategies*. Near such points the fitness landscape as experienced by a rare mutant is locally 'flat'. There are three qualitatively different ways in which this can occur as shown in Figure 3. Of these only the non-degenerate cases corresponding to fitness maxima and fitness minima are of interest here (because in degenerate cases finite evolutionary steps would lead past the local 'flatness'). The first, a fitness maximum, is known as an evolutionarily stable strategy (ESS) which, once established, cannot be invaded by nearby mutants. In contrast, Figure 3b shows a fitness minimum where disruptive selection will occur and the population branch into two morphs. This process, known as evolutionary branching, will be further discussed in Section 4.2.

In Figure 2 the singular strategies are found where the boundary of the region of positive invasion fitness intersects the diagonal. The first two PIPs show evolutionarily stable strategies (fitness maxima) since the invasion exponent is negative both above and below the singular strategy, while the third PIP shows a fitness minimum. A singular strategies that is attracting in the sense that nearby monomorphic populations can be invaded by mutants closer to the strategy is known as a convergence stable strategy (CSS). In Figure 2, only the two panels to the right (b and c) are convergence stable. There are four logical combinations of ESS and CSS and they can all be realised.

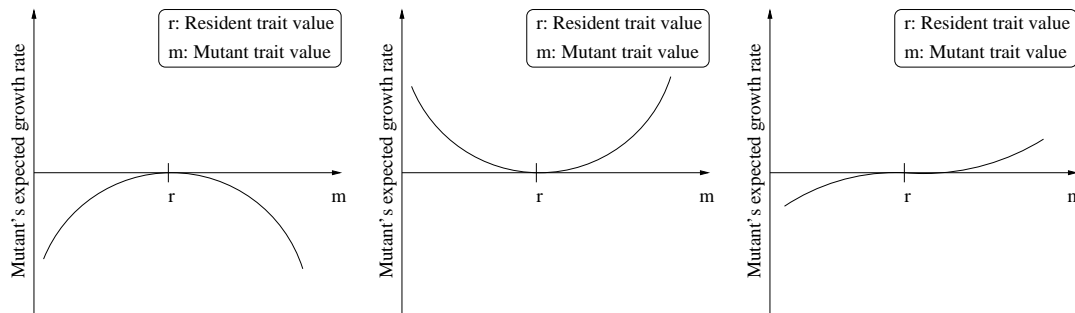


Figure 3: Three qualitatively different singular strategies: a) a local fitness maximum representing a possible endpoint of evolutionary change. b) Local fitness minimum where evolutionary branching can occur. c) A degenerate case where the criteria from section 3.3 fail because the second order derivative of $S_r(m)$ vanishes, but practically these cases are without significance, since finite evolutionary steps will lead evolution past these points. Fitness is defined here as the expected growth rate of an initially rare mutant and given by the invasion exponent.

If a strategy is both evolutionarily and convergence stable it represents a possible endpoint of evolutionary change, while a convergence stable strategy which is a fitness minimum is a branching point where the population will become dimorphic.

Singular strategies can be located and classified once the selection gradient is known. To locate singular strategies, it is sufficient to find the points for which the selection gradient vanishes, i.e. to find r^* such that $S'_{r^*}(r^*) = 0$. These can be classified then using the second derivative test from basic calculus. If the second derivative evaluated at r^* is negative (positive) the strategy represents a local fitness maximum (minimum). Hence, for an evolutionarily stable strategy r^* we have

$$S''_{r^*}(r^*) < 0 \quad (1)$$

If this does not hold the strategy is evolutionarily unstable and, provided that it also convergence stable, evolutionary branching will eventually occur. For a singular strategy r^* to be convergence stable monomorphic populations with slightly lower or slightly higher trait values must be invadable by mutants with trait values closer to r^* . That this can happen the selection gradient $S'_r(r)$ in a neighbourhood of r^* must be positive for $r < r^*$ and negative for $r > r^*$. This means that the slope of $S'_r(r)$ as a function of r at r^* is negative, or equivalently

$$\frac{d}{dr} S'_r(r) \Big|_{r=r^*} < 0. \quad (2)$$

The criterion for convergence stability given above can also be expressed using second derivatives of the invasion exponent, and the classification can be refined to span more than the simple cases considered here, as discussed in Appendix A.1 (see also Geritz et al., 1998). However, for practical purposes the concept of singular strategies as points where the invasion gradient vanishes and the basic criteria given by equations 1 and 2 for evolutionarily and convergence stability are often sufficient.

3.4. Jump processes and the canonical equation

The evolutionary process can be envisaged as a jump process: a sequence of successfully established mutant trait values together with the times at which the invasions occur. For large populations the process is directional as only mutants with positive initial growth rate can invade. This process can be simulated once explicit assumptions about the rate of mutations, the distribution of mutant trait values around the parent trait value and the establishment probability of mutants has been made. Mutations are often assumed to occur with a constant probability at each birth event, hence at a rate proportional to the birth rate, and mutant trait values often assumed normally distributed around the parent trait value. The establishment probability can either be determined from the model, or taken to be $\max(0, (b - d)/d)$ where b and d are the birth and death rates respectively. This is suggested by the theory of branching processes (see e.g. Grimmett & Stirzaker, 1992), where this is the probability that starting from one individual a population where individuals divide at a rate b and die at a rate d will not go extinct in finite time.

In Dieckmann & Law (1996) it is shown that when mutations are small, the evolutionary jump process can be approximated with a differential equation known as the canonical equation of Adaptive Dynamics. It states that the change of a resident trait in (evolutionary) time is proportional to the selection gradient,

$$r'(t) \propto S'_r(r) \quad (3)$$

where the constant of proportion is expressed in terms of the variance of the distribution of trait values. See Dieckmann & Law (1996) and Champagnat et al. (2001), for derivations and analyses.

4. Polymorphic evolution

The normal outcome of a successful invasion is that the mutant replaces the resident. However, other outcomes are also possible (Geritz et al., 2002), in particular both the resident and the mutant may persist and the population then becomes dimorphic. Assuming that a trait persists in the population if and only if its expected growth-rate when rare is positive, the condition for coexistence among two traits r_1 and r_2 is

$$S_{r_1}(r_2) > 0 \quad \text{and} \quad S_{r_2}(r_1) > 0,$$

where r_1 and r_2 are often referred to as *morphs*. Such a pair is a *protected dimorphism*. The set of all protected dimorphism is known as the *region of coexistence*. Graphically, the region consist of the overlapping parts when a pair-wise invasibility plot is mirrored over the diagonal (see Figure 4).

4.1. Invasion exponent and selection gradients in polymorphic populations

The invasion exponent is generalised to dimorphic populations in a straightforward manner, as the expected growth rate $S_{r_1, r_2}(m)$ of a rare mutant in the environment

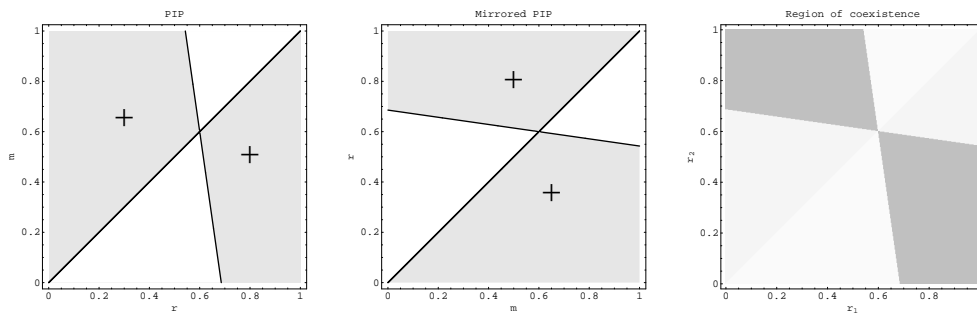


Figure 4: Illustration of the graphical method for obtaining the region of coexistence. a) A pairwise invasibility plot from the Snowdrift game (Hauert & Doebeli, 2004). b) The same pairwise invasibility plot mirrored over the main diagonal. c) The first two panels overlaid in which the region of coexistence is visible as the dark grey area. Note that protected dimorphisms are possible even though the singular strategy is evolutionarily stable and selection thus stabilising.

set by the two morphs r_1 and r_2 . The slope of the local fitness landscape for a mutant close to r_1 or r_2 is now given by the selection gradients

$$S'_{r_1, r_2}(r_1) \quad \text{and} \quad S'_{r_1, r_2}(r_2).$$

In practise, it is often difficult to determine the dimorphic selection gradient and invasion exponent analytically, and one often has to resort to numerical computations.

4.2. Evolutionary branching

The emergence of protected dimorphism near singular points during the course of evolution is not unusual, but its significance depends on whether selection is stabilising or disruptive. In the latter case, the traits of the two morphs will diverge in a process often referred to as evolutionary branching. Geritz et al. (1998) presents a compelling argument that disruptive selection only occurs near fitness minima. To understand this heuristically consider a dimorphic population r_1 and r_2 near a singular point. By continuity $S_r(m) \approx S_{r_1, r_2}(m)$ and, since $S_{r_1, r_2}(r_1) = S_{r_1, r_2}(r_2) = 0$, the fitness landscape for the dimorphic population must be a perturbation of that shown in Figure 3a with the region of positive invasion fitness lying between r_1 and r_2 .

4.3. Trait evolution plots

Evolution after branching is illustrated using trait evolution plots. These show the region of coexistence, the direction of evolutionary change and whether points where the selection gradient vanishes are fitness maxima or minima. Evolution may well lead the dimorphic population outside the region of coexistence, in which case one morph is extinct and the population once again becomes monomorphic.

Figure 5 shows an example of a trait evolution plot. The lines are *evolutionary isoclines* where one of the two selection gradients vanishes. These are found by solving

$$S'_{r_1, r_2}(r_1) = 0 \quad \text{or} \quad S'_{r_1, r_2}(r_2) = 0.$$

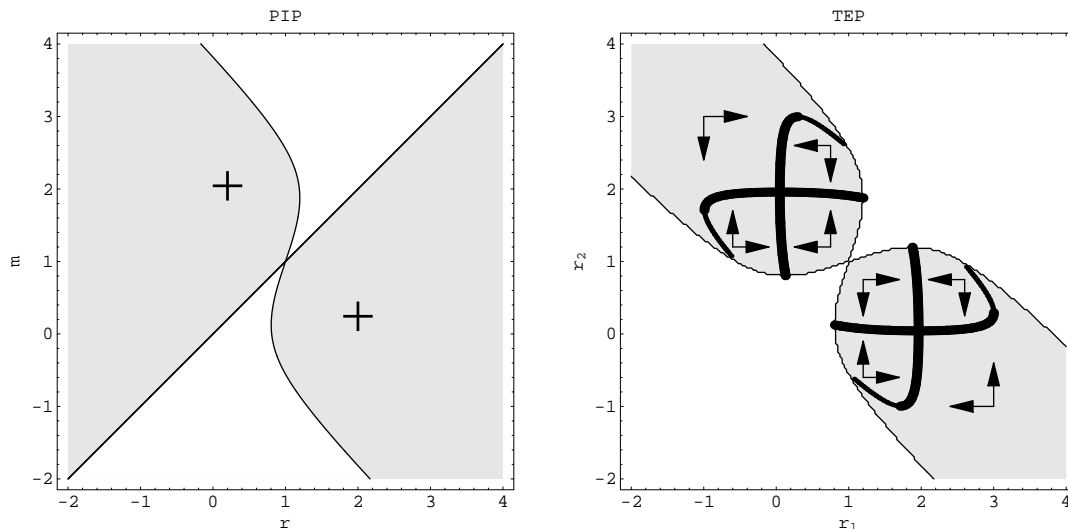


Figure 5: Levene's soft selection model studied by Geritz et al. (1998). The pairwise invasibility plot shows the evolutionary dynamics for a monomorphic population. Since selection at the convergence stable singular point is disruptive, the population eventually becomes dimorphic with evolutionary dynamics given by the trait evolution plot. The arrows show the direction of evolutionary change. Thick lines are evolutionarily stable isoclines, where directional selection in one of the two morphs cease. In this case, the trait evolution plot shows the final evolutionary outcome to be a stable protected dimorphisms with approximate trait values $r_1 = 2$ and $r_2 = 0$ where the ordering is arbitrary.

An isocline can be either a fitness maximum or fitness minima for mutants close to the morph (in fact the situation is exactly identical to the monomorphic case if we consider the other morph as being a constant part of the environment). We recommend using the same conventions as Geritz et al. (1998), that is using thin lines to denote fitness minima, and thick lines for fitness maxima.

4.4. Evolutionarily singular coalitions

An intersections of two isoclines at a point is known as a singular coalitions Geritz et al. (1998). If the strategies r_1 and r_2 at the intersection are stable strategies when considered separately with the other trait value fixed the coalition is stable and represent a possible endpoint where evolutionary change cease. To test for stability the analytical condition for evolutionary stability can be applied to each morph, however there is no natural generalisation of a CSS (Geritz et al., 1998) and convergence stability is most easily inferred directly from the trait evolution plot.

4.5. Connection of the isoclines to the boundary

The boundaries of the region of coexistence are extinction threshold for morphs, and hence for a dimorphic population r_1 and r_2 the boundary where r_2 becomes extinct is given implicitly by $S_{r_1}(r_2) = 1$ and for points in the region of coexistence close to

this boundary the approximate relationship $S_{r_1, r_2}(m) \approx S_{r_1}(m)$ holds. This simple observation has implications for the connection of the isoclines to the boundary. If $S'_{r_1, r_2}(r_1) = 0$ on the boundary we also have $S'_{r_1}(r_1) = 0$ so r_1 must be a singular point of a monomorphic population.

The isoclines defined by $S'_{r_1, r_2}(r_2) = 0$ connects to the boundary where it has a vertical tangent. The reason is that at every other point on the boundary, the selection gradient for r_2 points towards the interior of the region of coexistence (either up or down). If the isocline would connected to such a point it would divide the region into two areas where the selection gradient for r_2 points in opposing directions, and one of these would not be towards the interior which is a contradiction. By symmetry we get corresponding results for the other isoclines. For a more detailed discussion see Geritz et al. (1998)

4.6. Further evolutionary branching

Evolutionary branching in a morph r_1 under small but fixed mutational steps may occur whenever the fitness landscape as given by the function $S_{r_1, r_2}(m)$ has a local minimum at r_1 . The most likely branching point is an unstable singular coalition, but branching could also happen along an isocline.

5. Example

To clarify the basic concepts for monomorphic populations we now consider a population of n individuals where individuals reproduce at a rate b and die with the density-dependent rate dn . The number of individuals $n(t)$ at time t then grows logistically according to the linear differential equation $n'(t) = n(t)(b - n(t)d)$ subject to some initial condition $n(0) = n_0$. In particular the equilibrium population density n^* is found by solving $0 = n^*(b - dn^*)$ with the non-trivial solution $n^* = b/d$. Though not relevant here, it should be noted that a change of time-scale reduces the number of parameters to 1.

We will now assume that the birth-rate is subject to evolutionary change without constraint. The model must now be extended to include, at the very minimum, two populations n_1 and n_2 with respective trait values b_1 and b_2 . Writing $n(t) = n_1(t) + n_2(t)$ we have

$$n'(t) = b_1 n_1(t) + b_2 n_2(t) - dn(t)^2 \quad (4)$$

We now introduce the suggestive notation $n_r(t) = n_1(t)$, $r = b_1$ and $n_m(t) = n_2(t)$, $m = b_2$ for the respective trait values of the resident and mutant type. The invasion exponent is then defined as the initial per-capita growth rate of the mutant when it enters the equilibrium environment set by the mutant, which in this situation amounts to the logarithmic derivative of n_2 evaluated for $n_r = n^*$ and $n_m = 0$

$$S_r(m) = m - r.$$

Note that in particular $S_r(r) = 0$. The corresponding pair-wise invasibility plot is

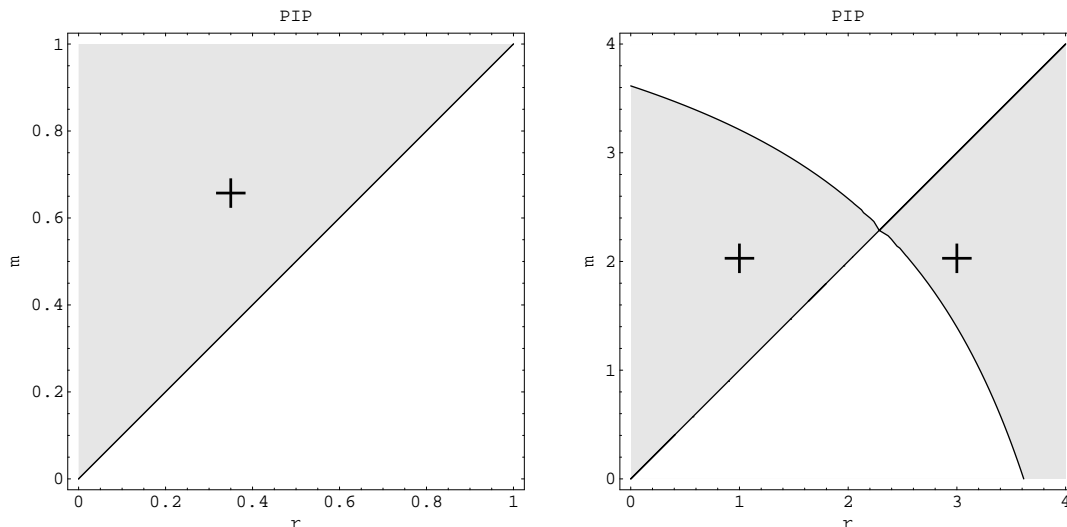


Figure 6: Pairwise invasibility plots of the example of a birth-death system. The relevant trait is the birth rate here. a) PIP according to the system given in (4). The birth rate can evolve to ever higher values. b) PIP according to the system given in 5 with $c(r) = 10^{-1} \exp(r)$. The singular point is evolutionarily and convergence stable and located at $r \approx 2.3$.

given in Figure 6a. As expected, the birth rate evolves towards ever higher values. We can change this by introducing a cost of higher birth rates

$$n'(t) = n(t)(r - c(r) - n(t)d) \quad (5)$$

yielding the invasion exponent

$$S_r(m) = m - c(m) - r + c(r).$$

Provided $b - c(b)$ is bounded we expect an evolutionary endpoint as a convergence and evolutionarily stable strategy according to criteria (1) and (2). For $c(r) = 10^{-1} \exp(r)$ we get the pairwise invasibility plot shown in Figure 6b with the singular point at $r = \ln(10) \approx 2.3$.

6. Discussion

The aim of this manuscript has been to introduce the basic concepts of Adaptive Dynamics. As with any introductory text, there are many issues that we have not touched upon. These include aspects of the treatment of higher dimensional traits, the problem of finding conditions for when a successfully invading mutant successfully ousts the resident, and the possibility of incorporating genetic detail. We have also left out any discussion of the implications of evolutionary branching—one of the most interesting findings of Adaptive Dynamics—for understanding speciation in sexually reproducing populations.

Even though there are many areas of Adaptive Dynamics which we haven't covered, the basic techniques are usually sufficient for practical purposes, and when not the material in this manuscript should be enough to read and understand many of the articles that advances or uses the theory.

7. Further reading

A good introductory text to Adaptive Dynamics is Dieckmann (2003), which presents the basics of monomorphic evolution using many instructive examples. The next natural step is Geritz et al. (1998) and Metz et al. (1996) which describe the theory in depth. To better understand how the techniques can be used in studying more complex models, a manuscript studying a sample model such as Geritz et al. (1999) or Brännström & Dieckmann (2005) may prove helpful.

The canonical equation is introduced by Dieckmann & Law (1996), studied in more detail by Champagnat et al. (2001) and extended to physiologically structured populations in Durinx & Metz (2005). Champagnat et al. (2006) puts this into context by considering ways in which microscopic stochastic processes can be studied on a macroscopic scale. Geritz et al. (2002) introduces the *Tube Theorem* which says that the sum of the resident and a sufficiently similar mutant populations canonically remain inside a 'tube'. Two more recent publications about the population dynamical foundations, basically the study of when a successfully invading mutant may be expected to replace the resident population, are Geritz (2003) and Gyllenberg et al. (2003). This is an active area of research, so please check the forward citations for the latest developments.

A list of articles related to Adaptive Dynamics is currently maintained by Éva Kisdi at <http://www.helsinki.fi/~mgyllenb/addyn.htm>. For an enjoyable evening read in front of the fireplace we recommend Leimar (2001) which argues that a 'Darwinian demon' able to control the mutations that occur can have a profound impact on evolution even if the actual population dynamics is beyond its control.

8. Acknowledgements

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9. About this document

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A. Appendix

A.1. Local classification of singular points

For a mathematical derivation of the criteria of ESS, CSS, and dimorphism we first need to conceive the invasion exponent $S_r(m)$ depending on m with the coefficient r as a function depending on two variables: $S_r(m) \equiv S(r, m)$. Both perspectives are exactly equivalent, but with the invasion exponent S seen as a map representing a two-dimensional fitness landscape as in the PIPs in Fig. 2 heuristic analytical arguments can easily be used for classification. We focus on the curvature of $S(r, m)$ landscape at singular points given in the second order derivatives following the argumentation of Geritz et al. (1998). The ESS criterion doesn't depend on the curvature in the direction of changed resident traits r and simply corresponds to the condition for a local maximum as argued in section 3.3

$$\left. \frac{\partial^2 S}{\partial m^2} \right|_{r=m=r^*} < 0 \quad (\text{ESS criterion}).$$

For a singular strategy to be CSS the selection gradient needs to point towards the singular strategy, i.e. its sign changes from positive to negative when going through r^* . So $S'_r(m)$ must be a decreasing function near the singular point

$$\frac{d}{dr} S'_r(r) = \left. \frac{\partial^2 S}{\partial r^2} \right|_{r=m=r^*} + \left. \frac{\partial^2 S}{\partial m \partial r} \right|_{r=m=r^*} < 0. \quad (6)$$

Since $S_r(r) = 0$ we have

$$0 = \left(\frac{d}{dr} \right)^2 S_r(r) = \left. \frac{\partial^2 S}{\partial r^2} \right|_{m=r} + 2 \left. \frac{\partial^2 S}{\partial m \partial r} \right|_{m=r} + \left. \frac{\partial^2 S}{\partial m^2} \right|_{m=r} \quad (7)$$

and thus (6) can be rewritten as

$$\left. \frac{\partial^2 S}{\partial r^2} \right|_{r=m=r^*} > \left. \frac{\partial^2 S}{\partial^2 m} \right|_{r=m=r^*} \quad (\text{CSS criterion}). \quad (8)$$

If a singular point is convergence stable but evolutionarily unstable, selection near the singular point is disruptive and evolutionary branching will eventually occur. However, even with stabilising selection protected dimorphism may occur near a singular point provided there are points near the singular strategy where both $S(r, m)$ and $S(m, r)$ are positive. This means that the line $m = 2r^* - r$ passing through the singular point at an angle of -45° must locally be in a region where S is positive. Thus, $S(r, 2r^* - r)$ must have a minimum at r^* meaning that at this point its second derivative is positive. Hence,

$$\left. \frac{\partial^2 S}{\partial m^2} \right|_{r=m=r^*} - 2 \left. \frac{\partial^2 S}{\partial r \partial m} \right|_{r=m=r^*} + \left. \frac{\partial^2 S}{\partial r^2} \right|_{r=m=r^*} > 0.$$

which using again (7) gives the criterion

$$\left. \frac{\partial^2 S}{\partial m^2} \right|_{r=m=r^*} > - \left. \frac{\partial^2 S}{\partial r^2} \right|_{r=m=r^*} \quad (\text{dimorphism criterion})$$

for protected dimorphisms to exist near the singular strategy.

A.2. Terms and concepts in brief

Term	Description
<i>invasion exponent</i>	Function giving the expected growth rate of a rare mutant
<i>selection gradient</i>	Derivative of the invasion exponent with respect to the mutant trait evaluated at the resident trait value. Gives information on the direction and speed of evolutionary change.
<i>Evolutionarily singular strategy</i>	Point or strategy where the selection gradient vanishes.
<i>Evolutionarily stable strategy</i>	Singular strategy that cannot be invaded by (locally) neighbouring mutants.
<i>Convergence stable strategy</i>	Singular strategy which, within a neighbourhood, is approached gradually.
<i>Monomorphic population</i>	Population consisting of only one phenotype.
<i>Dimorphic population</i>	Population with two phenotypes.
<i>Polymorphic population</i>	Population with several phenotypes.
<i>Pairwise invasibility plot</i>	Graphical illustration of invasion success for monomorphic populations.
<i>Trait evolution plots</i>	Graphical illustration of invasion success when the population is dimorphic.
<i>Canonical equation</i>	Differential equation describing a deterministic approximation of evolutionary dynamics with small mutational steps.

References

- Brännström, Å. & Dieckmann, U. (2005). Evolutionary dynamics of altruism and cheating among social amoebas. *Proceedings of the Royal Society series B*, **272**, 1609–1616.
- Champagnat, N., Ferrière, R., & Arous, G. B. (2001). The canonical equation of adaptive dynamics: A mathematical view. *Selection*, **2**, 73–83.
- Champagnat, N., Ferrière, R., & Méléard, S. (2006). Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models. *Theoretical Population Biology*. In press.

- Dieckmann, U. & Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology*, **34**, 579–612.
- Diekmann, O. (2003). A beginner's guide to adaptive dynamics. *Banach Center Publ.*, **63**, 47–86.
- Durinx, M. & Metz, J. A. J. (2005). Multi-type branching processes and adaptive dynamics of structured populations. In P. Haccou, P. Jagers, and V. A. Vatutin, editors, *Branching Processes: Variation, Growth and Extinction of Populations*, pages 266–277. Cambridge University Press.
- Falconer, D. S. & Mackay, T. F. C. (1996). *Introduction to quantitative genetics*. Prentice Hall.
- Geritz, S. A. H. (2003). Resident-invader dynamics and the coexistence of similar strategies. *Journal of Mathematical Biology*, **50**, 67–82.
- Geritz, S. A. H., Kisdi, E., Meszéna, G., & Metz, J. A. J. (1998). Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, **12**, 35–57.
- Geritz, S. A. H., van der Meijden, E., & Metz, J. A. J. (1999). Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology*, **55**, 324–343.
- Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A., & Parvinen, K. (2002). Invasion dynamics and attractor inheritance. *Journal of Mathematical Biology*, **44**, 548–560.
- Grimmett, G. R. & Stirzaker, D. R. (1992). *Probability and random processes*. The Clarendon Press Oxford University Press, New York, second edition.
- Gyllenberg, M., Jacobs, F. J. A., & Metz, J. A. J. (2003). On the concept of attractor for community-dynamical processes II: the case of structured populations. *Journal of Mathematical Biology*, **47**, 235–248.
- Hauert, C. & Doebeli, M. (2004). Spatial structure often inhibits the evolution of cooperation in the spatial snowdrift game. *Nature*, **428**, 643–646.
- Hofbauer, J. & Sigmund, K. (1998). *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge, UK.
- Leimar, O. (2001). Evolutionary change and darwinian demons. *Selection*, **2**, 65–72.
- Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A., & van Heerwaarden, J. S. (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In S. J. van Strien and S. M. V. Lunel, editors, *Stochastic and spatial structures of dynamical systems*. North Holland, Amsterdam.
- Roughgarden, J. (1979). *Theory of Population Genetics and Evolutionary Ecology: an introduction*. Macmillan Publishing Co., Inc.