Adaptive Dynamics 19/11/2010

Johan Metz

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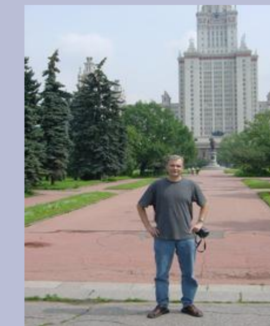
20 Questions on Adaptive Dynamics



doi:10.1111/j.1420-9101.2005.00948.x

TARGET REVIEW

20 Questions on Adaptive Dynamics

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Keywords:

Adaptive Dynamics;
assortative mating;
evolution;
population genetics;
speciation;
theory.

Abstract

Adaptive Dynamics is an approach to studying evolutionary change when fitness is density or frequency dependent. Modern papers identifying themselves as using this approach first appeared in the 1990s, and have greatly increased up to the present. However, because of the rather technical nature of many of the papers, the approach is not widely known or understood by evolutionary biologists. In this review we aim to remedy this situation by outlining the methodology and then examining its strengths and weaknesses. We carry this out by posing and answering 20 key questions on Adaptive Dynamics. We conclude that Adaptive Dynamics provides a set of useful approximations for studying various evolutionary questions. However, as with any approximate method, conclusions based on Adaptive Dynamics are valid only under some restrictions that we discuss.

And the commentaries...

Commentaries

Jump to...

Useful ways of being wrong (pages 1155–1157)
H. KOKKO
Article first published online: 25 AUG 2005 | DOI: 10.1111/j.1420-9101.2004.00853.x
Abstract | Full Article (HTML) | PDF(50K) | References

The future of a mutation-limited tool-box (pages 1158–1161)
T. J. M. VAN DOOREN
Article first published online: 25 AUG 2005 | DOI: 10.1111/j.1420-9101.2005.00881.x
Abstract | Full Article (HTML) | PDF(57K) | References

'Adaptive Dynamics' vs. 'adaptive dynamics' (pages 1162–1165)
P. A. ABRAMS
Article first published online: 25 AUG 2005 | DOI: 10.1111/j.1420-9101.2004.00843.x
Abstract | Full Article (HTML) | PDF(58K) | References

Wright meets AD: not all landscapes are adaptive (pages 1166–1169)
M. KIRKPATRICK and F. ROUSSET
Article first published online: 25 AUG 2005 | DOI: 10.1111/j.1420-9101.2004.00847.x
Abstract | Full Article (HTML) | PDF(74K) | References

Adaptive dynamics and the paradigm of diversity (pages 1170–1173)
É. KISDI and M. GYLLENBERG
Article first published online: 25 AUG 2005 | DOI: 10.1111/j.1420-9101.2004.00852.x
Abstract | Full Article (HTML) | PDF(59K) | References

Seven answers from adaptive dynamics (pages 1174–1177)
S. A. H. GERITZ and M. GYLLENBERG

And some background reading...

Adaptive Dynamics Papers

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- Special issues
- Diversification without speciation
- Genetics and speciation
- Applications
- Forerunners
- Other approaches

ADAPTIVE DYNAMICS PAPERS

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Eshel, I., U. Motro, and E. Sansone. 1997. Continuous stability and evolutionary convergence. J. theor. Biol. 185:333-343.

> *The first paper above gives a self-contained description of the adaptive dynamics framework and an illustrative example for how it can be used. The second paper is a short account specifically tailored for the interest of physicists; the third paper is more mathematical. Eshel et al. reached some of the results independently.*

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Kisdi É. & M. Gyllenberg. 2004. On some misconceptions about adaptive dynamics. TUCS Technical Report 624 (ISBN 952-12-1417-1)

Meszéna G., M. Gyllenberg, F. J. Jacobs & J. A. J. Metz. 2005. Link between population dynamics and dynamics of Darwinian evolution. Phys. Rev. Letters PRL 95, 078105.

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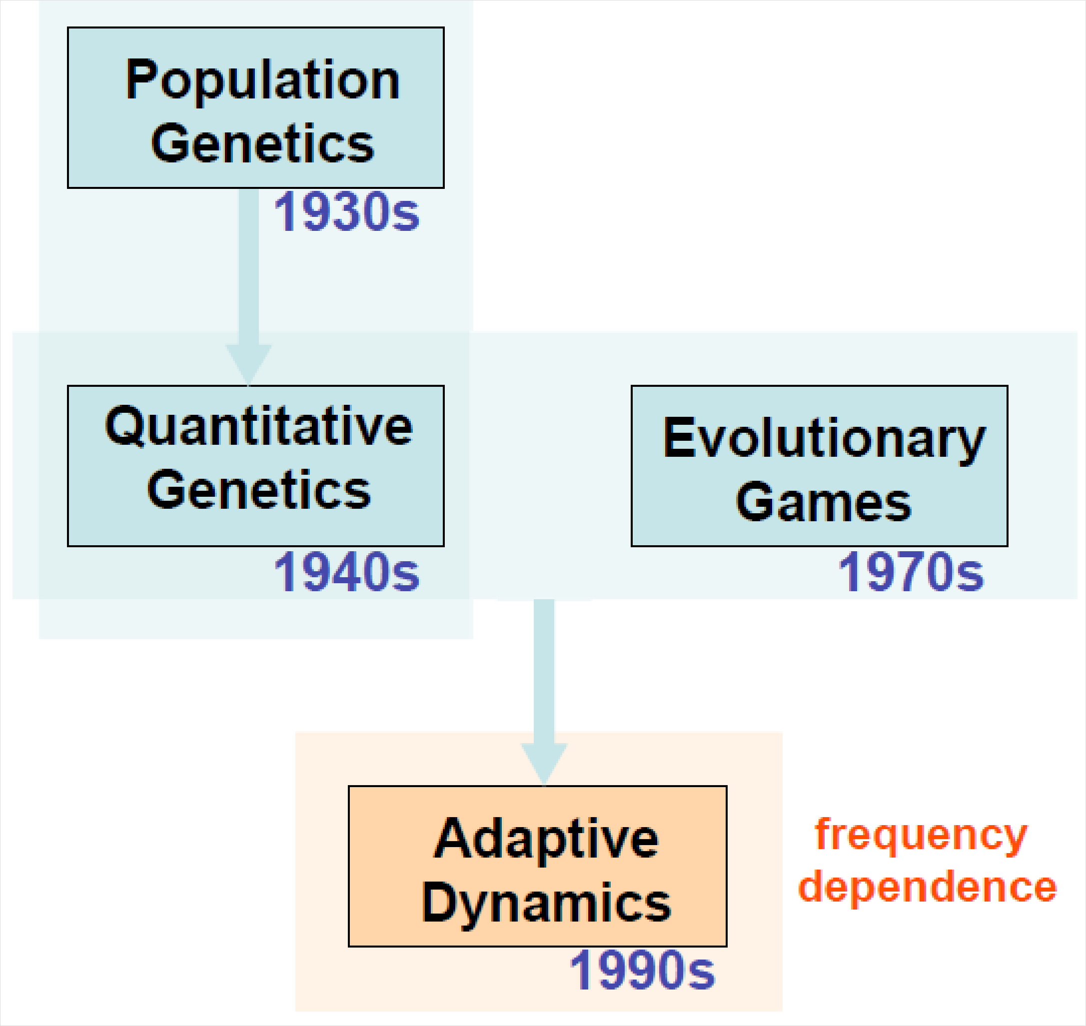
Historical background



Modelling approaches to evolutionary dynamics

Table 2.4 Comparison of modeling approaches to evolutionary dynamics.

approach	geno-type	pheno-type	short-term	long-term	evol. tree	det. mod.	stoch. mod.
population genetics*	✓		✓			✓	✓
individual-based evolutionary models	✓	✓	✓	✓	✓		✓
quantitative genetics		✓	✓			✓	
evolutionary game theory		✓				✓	
replicator dynamics		✓	✓			✓	
fitness landscapes		✓		✓		✓	
adaptive dynamics		✓		✓	✓	✓	✓

*classical formulation only: short-term evolution of genotypic distributions.

Dercole, F. and Rinaldi S. (*2008)*, *Analysis of evolutionary processes* PSTCB

Q1 What is adaptive dynamics?

- Adaptive dynamics describes the long-term evolutionary dynamics of continuously varying traits, by explicitly taking into account the resident-mutant demographic interactions underlying the process of selection.

- The theorem of adaptive dynamics has been proved under the following technical conditions:

  - Spatial heterogeneity and physiological structures (age, stage etc) of resident and mutant populations are not described, so that the resident-mutant model is composed of one equation for each population.

  - Stationary coexistence of the resident populations

  - The community is composed of a single resident population characterized by mutations with effects on many traits, or of many resident populations characterized by mutations which only influence a single scalar trait.

- In short:
  - Mutations occur rarely and cause very small changes in existing phenotypic values.
  - Assumes phenotypic evolution under clonal reproduction (i.e., no genes, no sex).
  - Separation of ecological and evolutionary time scales.
  - Small initial mutant frequency in a large resident population.

The AD modeller's tool kit!

- Invasion fitness
- Pairwise invasibility plots
- The canonical equation of adaptive dynamics

Q2 How are fitness functions derived in adaptive dynamics?

- Basic population genetics models use fitness functions that depend only on the phenotypic trait values under selection.

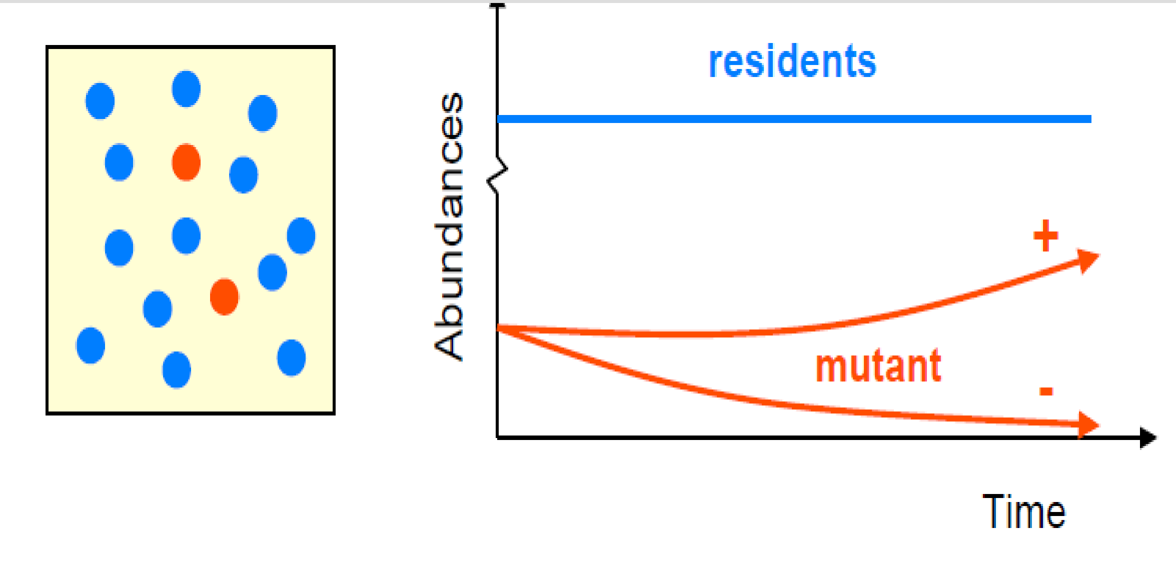
- In reality, fitness is dependent upon (from ecology):
  - The frequencies of individuals with different trait values
  - The density of the population (e.g., ind. per unit area)
  - The absolute number of individuals in the population.

- Adaptive Dynamics attempts to combine the two

Waxman and Gavrilets, J. Evol. Biol. (2005)

Q3 What is invasion fitness?

- The fitness function of very rare mutants with phenotype 'y', in an (almost monomorphic) resident population with phenotype 'x' is typically written as s(y,x), or $S_x(y)$. NB often y is replaced by x'
- Its precise form depends on the biological situation under consideration.
- S is defined as the long-term per capita growth rate of a rare variant in an environment determined by one or more residents.
- With **s(x,x)=0**, the mutant population will typically grow exponentially if **s(y,x) >0**, or decay exponentially if **s(y,x) <0**.



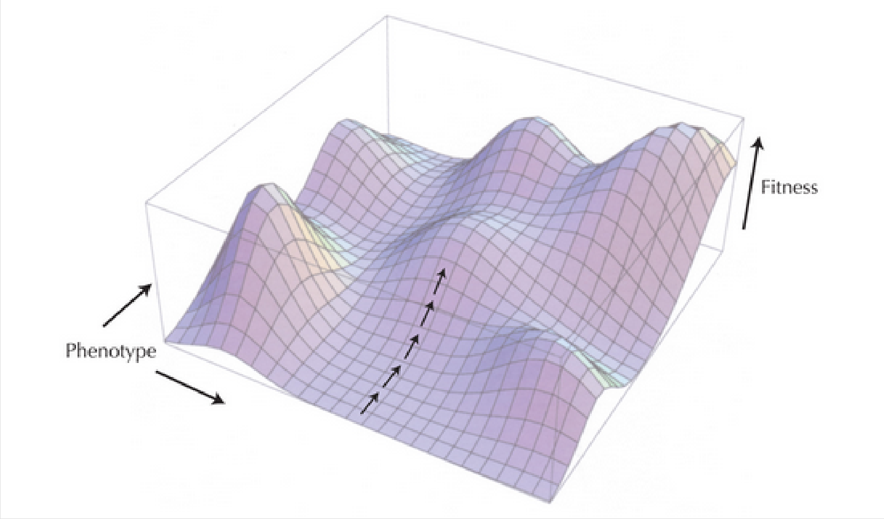
Waxman and Gavrilets, J. Evol. Biol. (2005); Meric, A Pers. Comm.

Q4 What is an invasion fitness landscape?

- If fitness depends only on the trait values of an individual, the fitness landscape remains rigid and unchanging.

- If fitness is density or frequency dependent, the fitness landscape heaves and bulges as the population moves over it

Fitness landscape



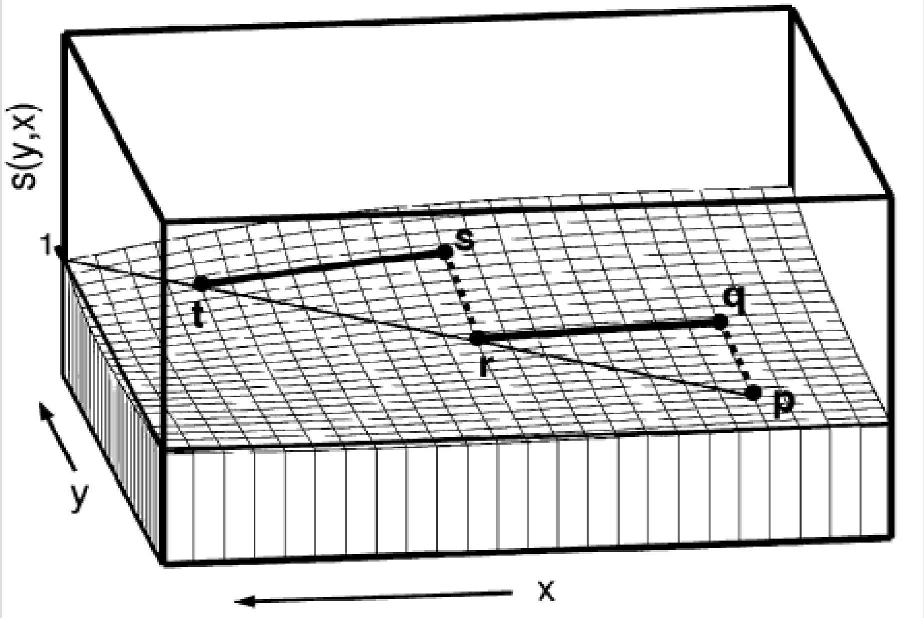
Waxman and Gavrilets, J. Evol. Biol. (2005)

Q4 What is an invasion fitness landscape?

- An invasion fitness landscape is a **fixed** landscape (even when fitnesses are density/frequency dependent), and is thus fundamentally different to a traditional fitness landscape.

- In addition, instead of moving uphill over the landscape, the population tracks a path among the hills, where s(y,x)=0.

Invasion fitness landscape



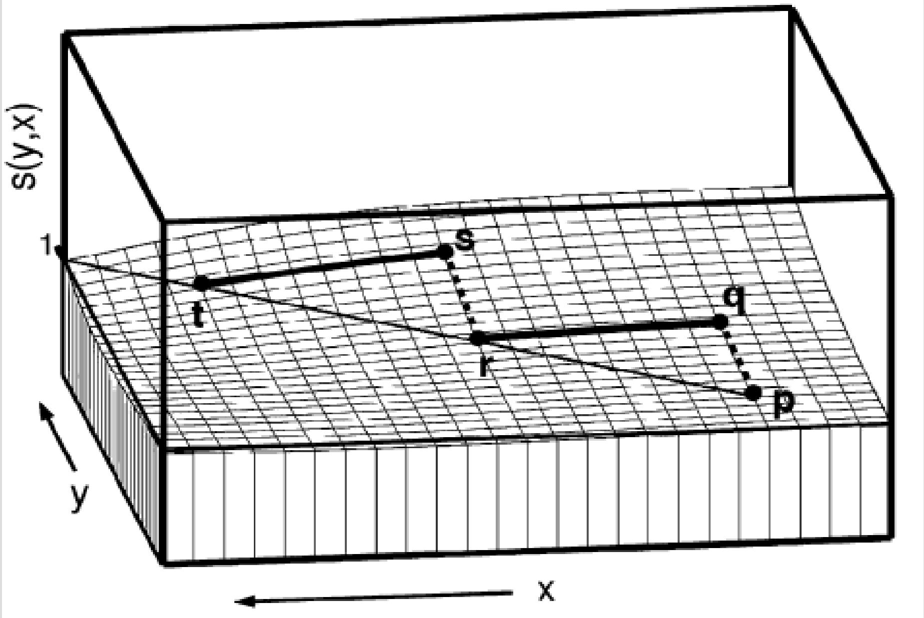
- x-axis: resident phenotype (x)
- y-axis: mutant phenotype (y)
- z-axis: s(y,x)

Waxman and Gavrilets, J. Evol. Biol. (2005)

Q5 How does the population move on the invasion fitness landscape?

- Assume |x-y| is small, i.e., most mutations are of small effect.
- Then, for a resident population with phenotype x (**point p**), a mutant, with phenotype y (**point q**) will invade and replace the resident if s(y,x)>0.
- The resident phenotype is then reset to y, i.e., x=y (**point r**).
- For mutations with a small effect, the population will roughly track along the line y=x.

Invasion fitness landscape

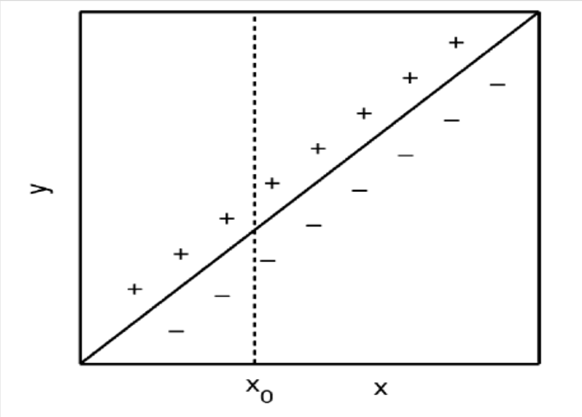


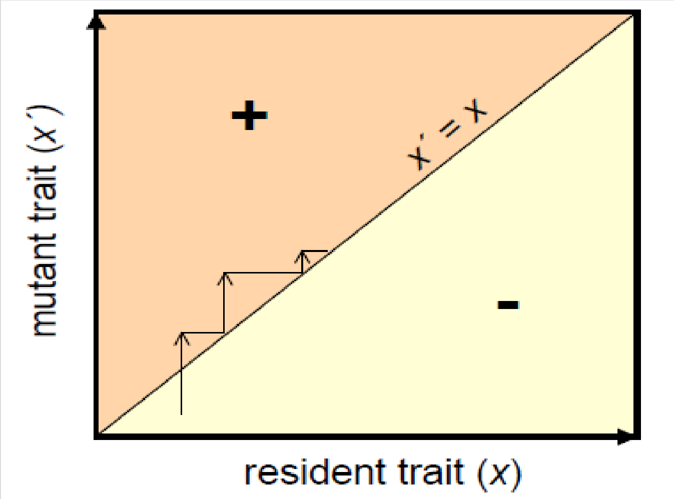
- x-axis: resident phenotype (x)
- y-axis: mutant phenotype (y)
- z-axis: s(y,x)

Waxman and Gavrilets, J. Evol. Biol. (2005)

Q7 What are pair-wise invasibility plots?

- A horizontal slice taken through the invasion fitness landscape at s(y,x)=0.
- In regions marked with '+' signs, mutants have a fitness greater than that of the resident and can invade.
- As |y-x| is assumed to be small, attention falls on the region around the line y=x.
- Can be pictured as a 'stair climbing process'

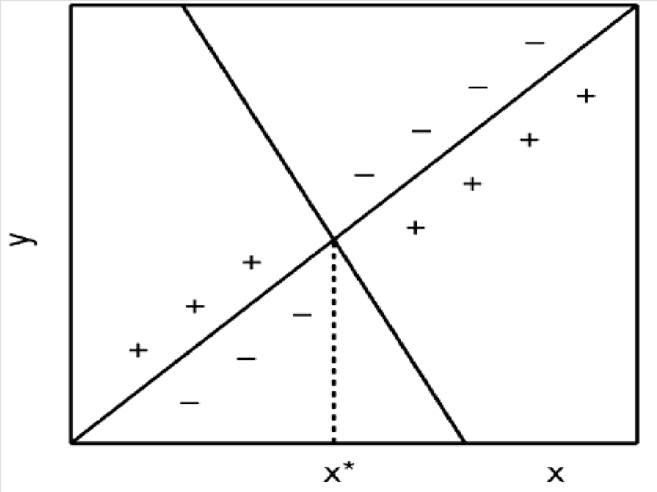


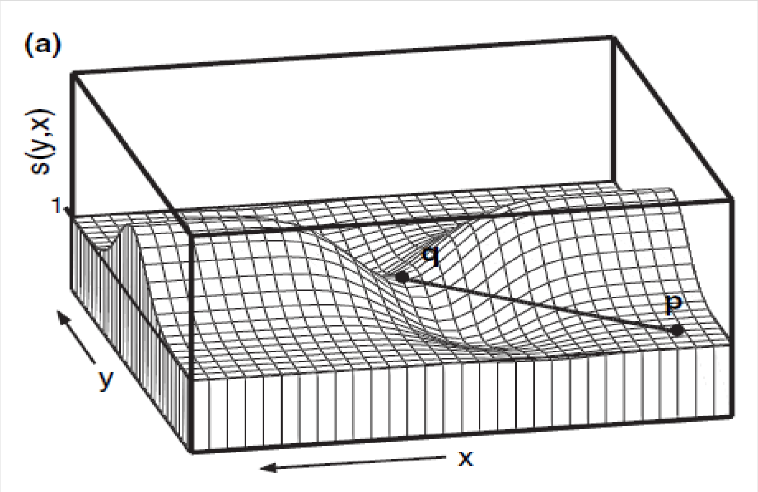


Waxman and Gavrilets, J. Evol. Biol. (2005); Meric, A Pers. Comm.

Q8 Evolutionary singular strategies

- Here it is assumed there is a second curve (in addition to y=x) on which s(y,x) - s(x,x) = 0.
- The intersection point is x*, at which D(x) = 0.
- This is termed an '***Evolutionary Singular strategy***'
- The point x* shown here in fact corresponds to the point q on the fitness landscape.





Waxman and Gavrilets, J. Evol. Biol. (2005); Meric, A Pers. Comm.

Q8 What evolutionary singular strategies are possible?

- At x*, the first-order derivative of s(y,x) wrt to both x and y vanishes.
- Different types of evolutionary singular strategies may be identified by the first non-vanishing derivatives (generically second order).
- There are 8 different possible types of ESS.

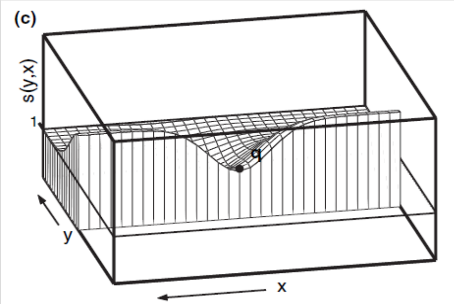
$$A = \left[\frac{\partial^2 s(y,x)}{\partial x^2}\right]_{x=x^*, y=x^*}, \qquad B = \left[\frac{\partial^2 s(y,x)}{\partial y^2}\right]_{x=x^*, y=x^*}$$

$$\mathrm{sign}(x) = \begin{cases} +1, & \text{when } x > 0, \\ -1, & \text{when } x < 0. \end{cases}$$

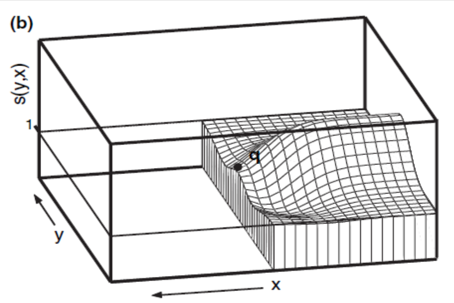
We then define

$$a = \mathrm{sign}(A), \quad b = \mathrm{sign}(B), \quad c = \mathrm{sign}(|A| - |B|).$$

A



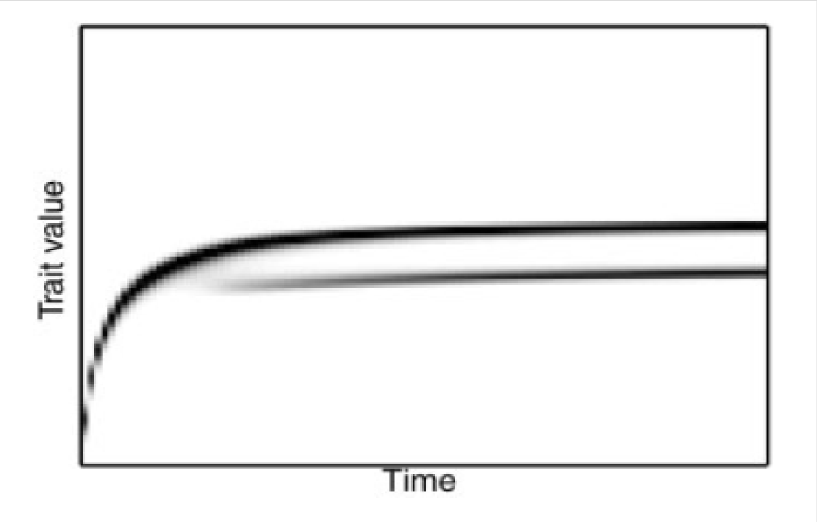
B

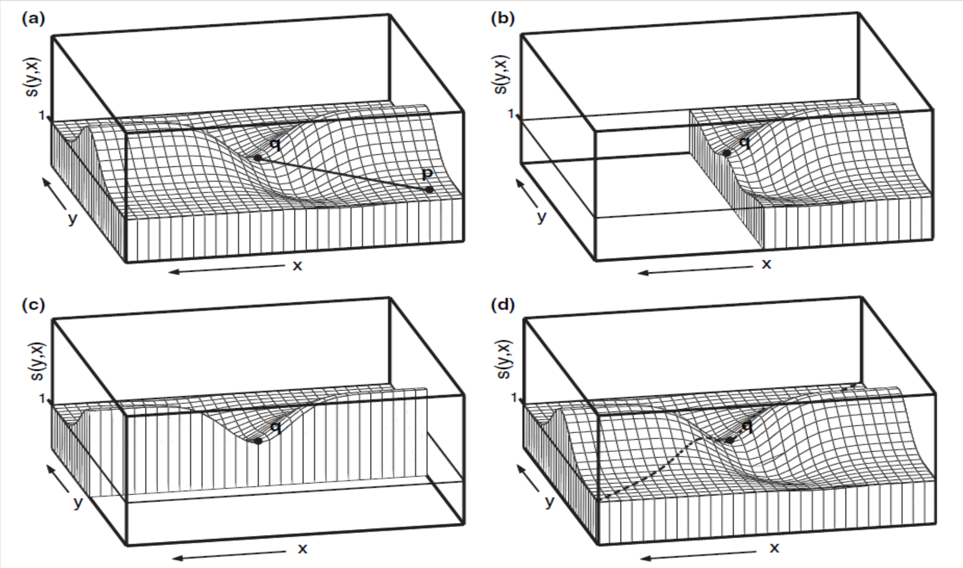


Q9 What are evolutionary branching points?

- An evolutionary singlular strategy is an evolutionary branching point if:
  - It is invasible
  - Is able, when rare, to invade another nearby strategy
  - Is convergence stable
  - Has protected polymorphisms

- May occur when a population is evolving toward x*, then a mutant is introduced with a trait y on the opposite side of x* to the resident.





The canonical equation of adaptive dyamics

$$\frac{d}{dt}s_i = k_i(s) \cdot \frac{\partial}{\partial s_i'} W_i(s_i', s) \Big|_{s_i' = s_i}$$

- Where
  - s_i denotes adaptive trait values in a community
  - W(s'_i,s) are measures of fitness of individuals with trait value s'_i in an environment determined by resident trait values s.
  - k_i(s) are non-negative coefficients that scale the rate of evolutionary change.

- The canonical equations describes the long-term evolution of reproductively isolated monomorphic populations, a description that fits with the case of a-sexual reproduction, or non-interbreeding sexual populations.

For easy examples, see...

MATHEMATICAL MODELLING OF
POPULATION DYNAMICS
BANACH CENTER PUBLICATIONS, VOLUME 63
INSTITUTE OF MATHEMATICS
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WARSZAWA 2004

A BEGINNER'S GUIDE TO ADAPTIVE DYNAMICS

ODO DIEKMANN

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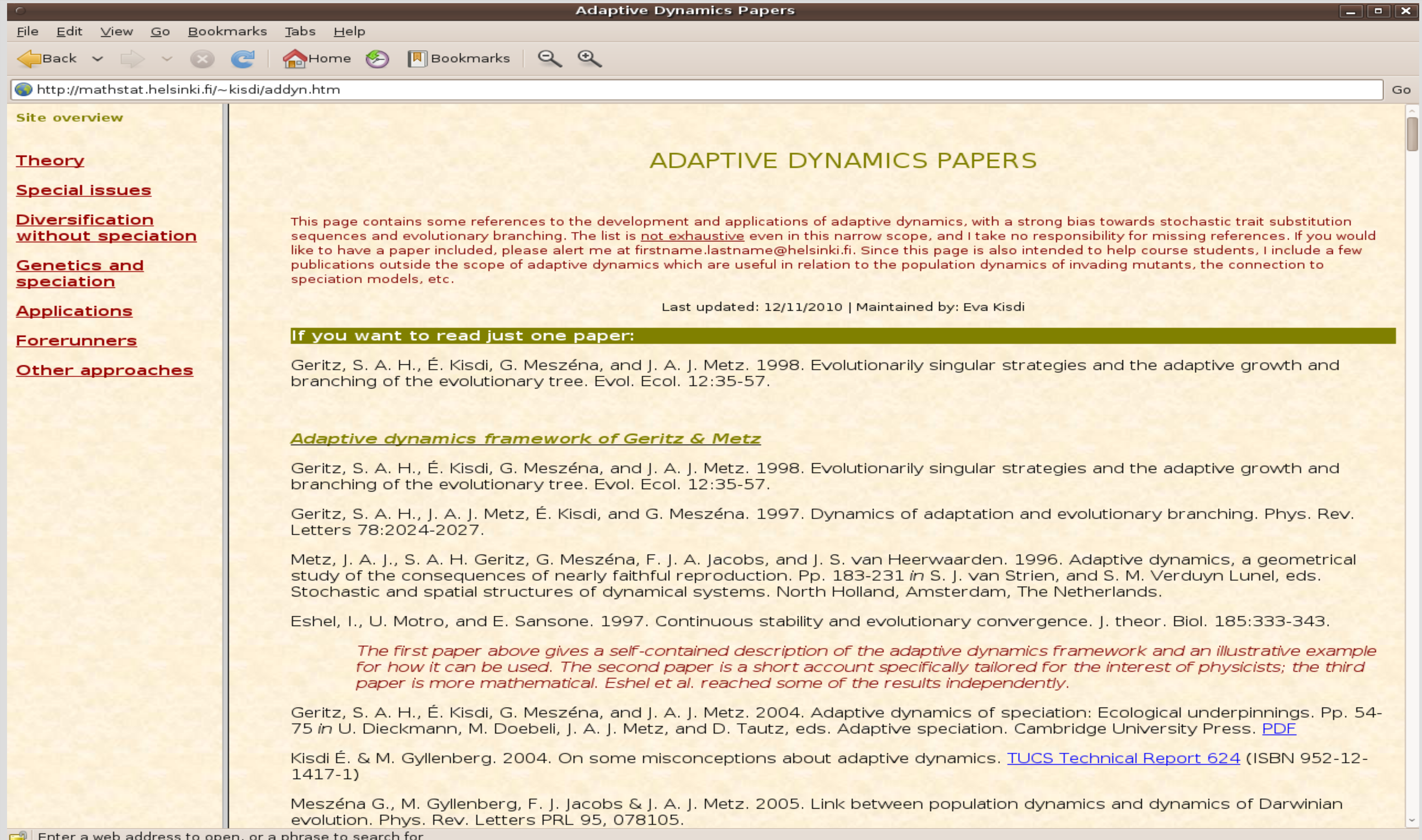
Abstract. The aim of these notes is to illustrate, largely by way of examples, how standard ecological models can be put into an evolutionary perspective in order to gain insight in the role of natural selection in shaping life history characteristics. We limit ourselves to phenotypic evolution under clonal reproduction (that is, we simply ignore the importance of genes and sex).

Further reading...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