DYAD
Master EBE M2

# Adaptive dynamics II: pairwise invasibility plots, canonical equation, classification of singular points

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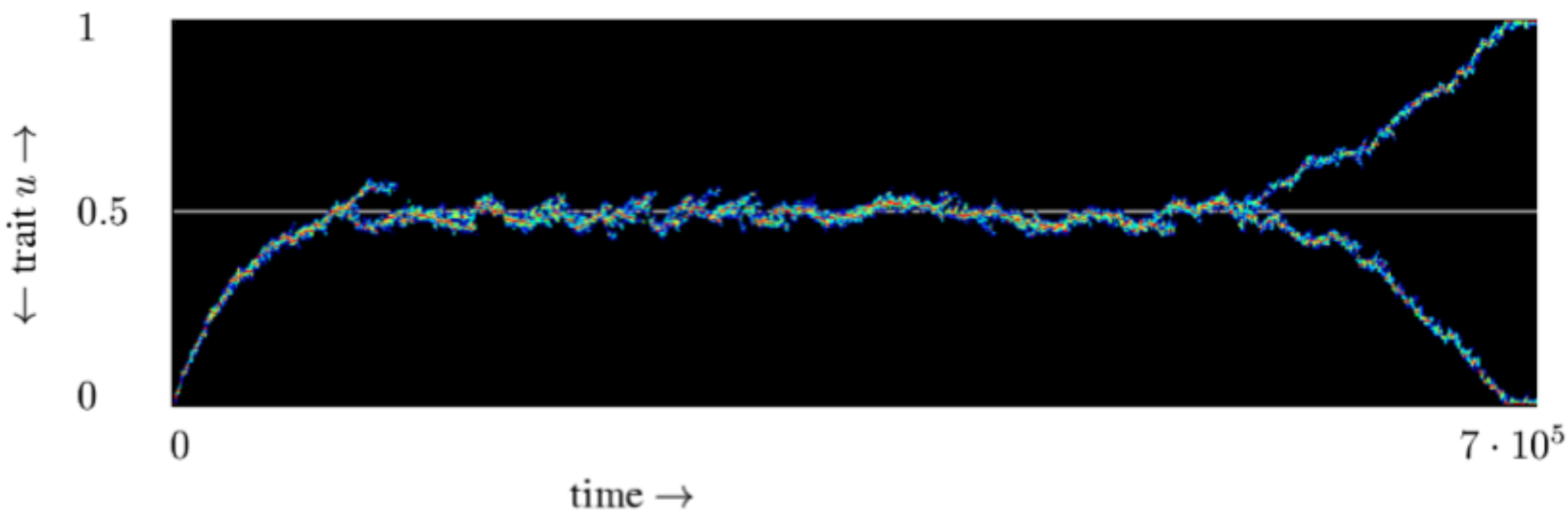
# OBJECTIF

- Une théorie quantitative pour prédire la *tendence evolutive* (a trajectoire), et les *equilibres* de l'evolution
- Contexte écologique : *fitness* est supposé être determiné par d'interactions écologiques



# MECHANISTIC THEORY OF EVOLUTION

- 1850 Darwin "On the origins of species" (1859)
  - "Struggle for existence": evolution is driven by interactions between individuals
  - But a flaw: "blending inheritance"
- 1880-1900 Mendel (re-discovered by Hugo de Vries)
  - Inheritance by genes
- 1920s "*Neo-Darwinism*"
  - Fisher, Haldane, Wright
  - reconciliation of Darwin and Mendel
- 1940-1950s "*Modern Synthesis*"
  - Paleontology, taxonomy
  - Theory: population genetics
    - Realistic models of inheritance
    - Focus on relative allele frequencies, fixed gene-repertoire,
    - Non-interacting individuals
- 1970s game theory (ESS)
- 1990s adaptive dynamics

# EUS AND ESS

- Hamilton (1967), Maynard-Smith and Price (1973)
  - EUS = Evolutionary Unbeatable Strategy
  - ESS = Evolutionarily Stable Strategy
    - a strategy which, when played by everybody, prevents all comparable strategies from increasing in abundance
  - Evolutionary trap
  - Particular shape of the "*fitness function*", or: the "*adaptive landscape*"
- But…
  - Usually only clonal reproduction
  - Only **end-point** of evolution, not the **dynamics**

- Adaptive dynamics:
  - Dynamic counterpart to the EUS concept

# ADAPTIVE DYNAMICS

- Metz, Eshel, Christiansen, Taylor, Sigmund, Roughgarden, Hammerstein…
  - Geritz, Jacobs, Dieckmann, Ferriere, Hofbauer, Rinaldi, etc
- Roots in ecology:
  - fitness is derived from a model of ecological dynamics and ecological interactions (competition, predation, mutualism, etc)
- "Individual-based" approach
  - individual → population dynamics → selection → individual
- Original formulation (Metz et al 1996), basic assumptions:
  - Clonal reproduction
  - Large population size, rare mutations
  - Unique and global attractor of the population dynamics

# TRAITS

- "Trait" or "evolving trait"
  - = the phenotypic trait that is assumed to be evolving
  - Often all other phenotypic traits are assumed to remain constant
- Numerical traits such as
  - Body size (length, mass, volume)
    - Ex: body size at maturation
  - Fecundity, survival
  - Resource utilisation (specialisation)
- "Type" = individual(s) with a certain trait value

- Monomorphic vs. polymorphic
  - Monomorphic = all individuals in the population have the same trait value
  - Polymorphic = there are 2 or more types (are coexisting in the population.

# FITNESS

- Definition :
  - The asymptotic average rate of exponential growth of a small population of type $x$ in a given environment E

$$f = \lim_{t \to \infty} \frac{1}{t} \ln \frac{N(t)}{N(0)}$$

  - The given environment E depends on the ecological dynamics of the currently existing ecological community

- Resident = the current population, into which mutants arrive
  - The background for evaluating invasion fitness

# INVASION FITNESS - EXAMPLE

- Stochastic individual-based model
  - "Branching process"
  - "Birth-death process"
- Each individual gives birth with rate B
- Each individual dies with rate D
- Expected per capita rate of increase $r$ = B-D
  - If $r<0$ then extinction with probability $P_{ext}=1$
  - If $r>0$ then extinction with probability $P_{ext}<1$, exponential growth ("invasion") with probability $(1-P_{ext})>0$

# RESIDENTS AND MUTANTS (PART 1)

- Simple case: assume a monomorphic resident population of type $x$
- The resident population is in its stationary state corresponding to its trait $x$
  - Equilibrium, limit cycle, chaotic dynamics
- The environment $E$ represents the ecological interactions (density-dependent)
  - Ex: Food density, available space, available mates
- A mutant arrives, of type $x'$
  - Its or fitness is thus: $f(x', E_x)$ or, more shortly: $f(x', x)$

mutant, resident

# RESIDENTS AND MUTANTS (PART 2)

mutant, resident

- If $f(x', x) > 0$ then the mutant *can* invade
- If $f(x', x) < 0$ then the mutant will go extinct

- What happens after invasion?

- Consider the hypothetical case that the mutant has become the resident, and the ex-resident tries to invade.

- If $f(x, x') > 0$ then the ex-resident can invade
- If $f(x, x') < 0$ then the ex-resident will go extinct

# RESIDENTS AND MUTANTS (PART 3)

We can now distinguish different cases

- $f(x', x) < 0$
  - The mutant cannot invade (goes extinct)
- $f(x', x) > 0$ and $f(x', x) < 0$
  - The mutant can invade and replaces the ex-resident
- $f(x', x) > 0$ and $f(x', x) > 0$
  - The mutant can invade and the co-exists with the resident
  - "*Mutual invasibility*"

# TRAIT SUBSTITUTION SEQUENCE

- Direction evolution (by directional selection)
- A sequence of invasions of mutants, followed by replacement.
  - Resident $x=0.1 \rightarrow$ mutant $x=0.12$ replaces
  - Resident $x=0.12 \rightarrow$ mutant $x=0.13$ replaces
  - Resident $x=0.13 \rightarrow$ mutant $x=0.15$ replaces
  - etc…
- Assumption: mutation limited evolution
  - separation of time scales
    - <u>Fast</u> ecological dynamics
    - <u>Slow</u> evolutionary dynamics
- Questions:
  - How fast does the trait evolve?
  - What is its trajectory? (The "*course*" of evolution)
  - Where does it stop? (Does it stop?) What happens next?

# INVASION FITNESS - EXAMPLE

- Lotka-Volterra competition

$$\frac{dN_i}{dt} = rN_i \left( 1 - \frac{\sum_j a(x_i, x_j) N_j(t)}{K(x_i)} \right)$$

$N_i$ = abundance pop i

$x_i$ = trait of pop i

a(x,y) = competition coefficient; impact of type y on type x

- Rare mutant of type x', resident types *j* at equilibrium

$$\frac{1}{N'} \frac{dN'}{dt} = r \left( 1 - \frac{\sum_j a(x', x_j) \hat{N}_j}{K(x')} \right)$$

equilibrium abundance of pop j

- Rare mutant of type x' in monomorphic resident of type x ($N_{res}=K(x)$)

$$f(x', x) = r \left( 1 - a(x', x) \frac{K(x)}{K(x')} \right)$$

# THE CANONICAL EQUATION (V1)

- *Unstructured populations*
- The speed of directional evolution

$$\frac{dx}{dt} = \frac{1}{2}\alpha(x)\mu(x)N(x)(\sigma_m(x))^2 \left.\frac{\partial f(x',x)}{\partial x'}\right|_{x'=x}$$

# THE COURSE OF EVOLUTION

- Directional selection
  - $dx/dt > 0$ or $<0$

- Evolutionary singular strategies
  - $dx/dt = 0$
  - What happens?

- Graphical tool: PIP
  - Pairwise Invasibility Plot

  - Works very well for 1-dim traits
  - Does not work (well) for traits of dim 2 and higher

# PIP (PAIRWISE INVASIBILITY PLOT)

38 *Geritz* et al.

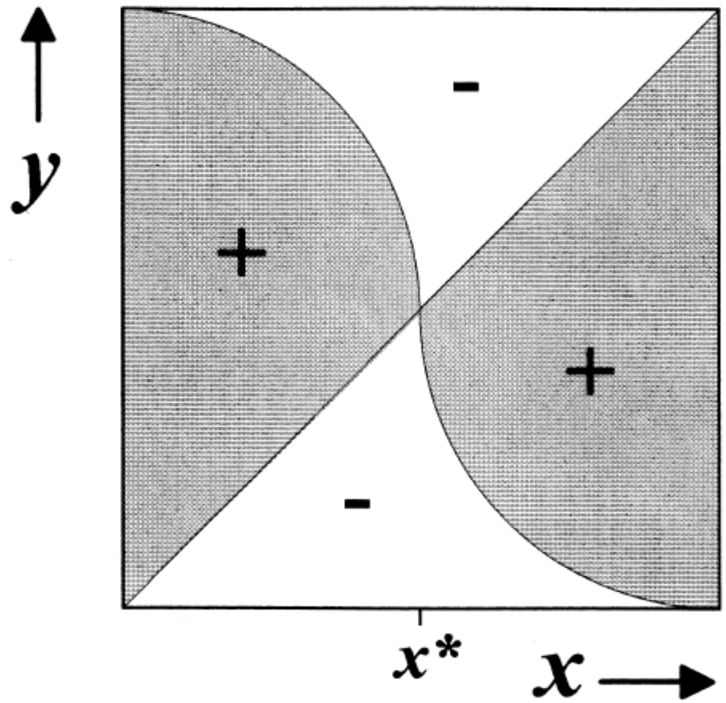
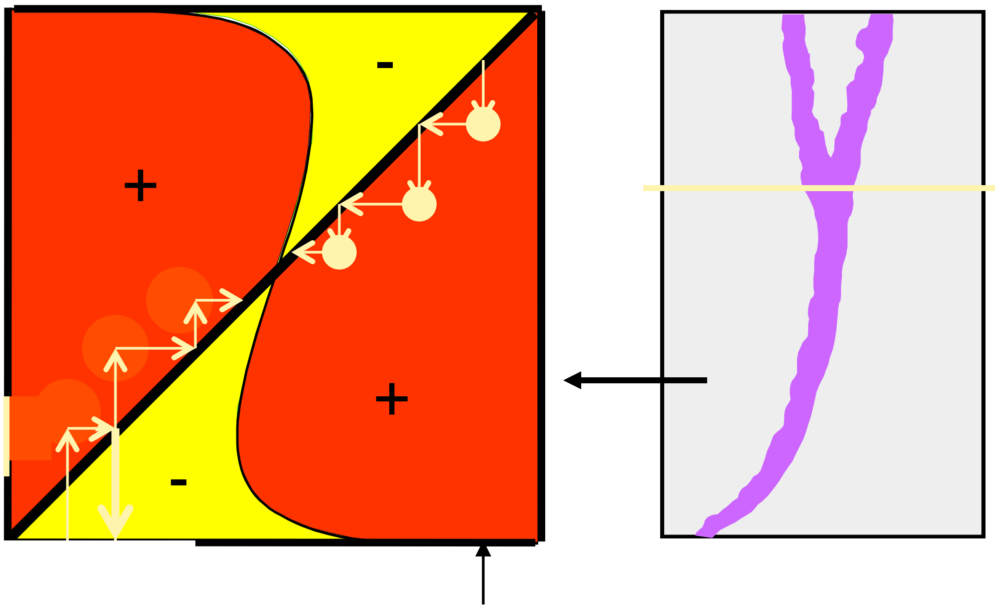



Figure 1. Example of a pairwise invasibility plot. The resident's and mutant's strategy are denoted by $x$ and $y$, respectively. The shaded area indicates combinations of $x$ and $y$ for which the mutant's fitness, $s_x(y)$, is positive. The singular strategy is denoted by $x^*$.

# A bit more adaptive dynamics theory for later reference

fitness contour plot
x: resident
y: potential mutant



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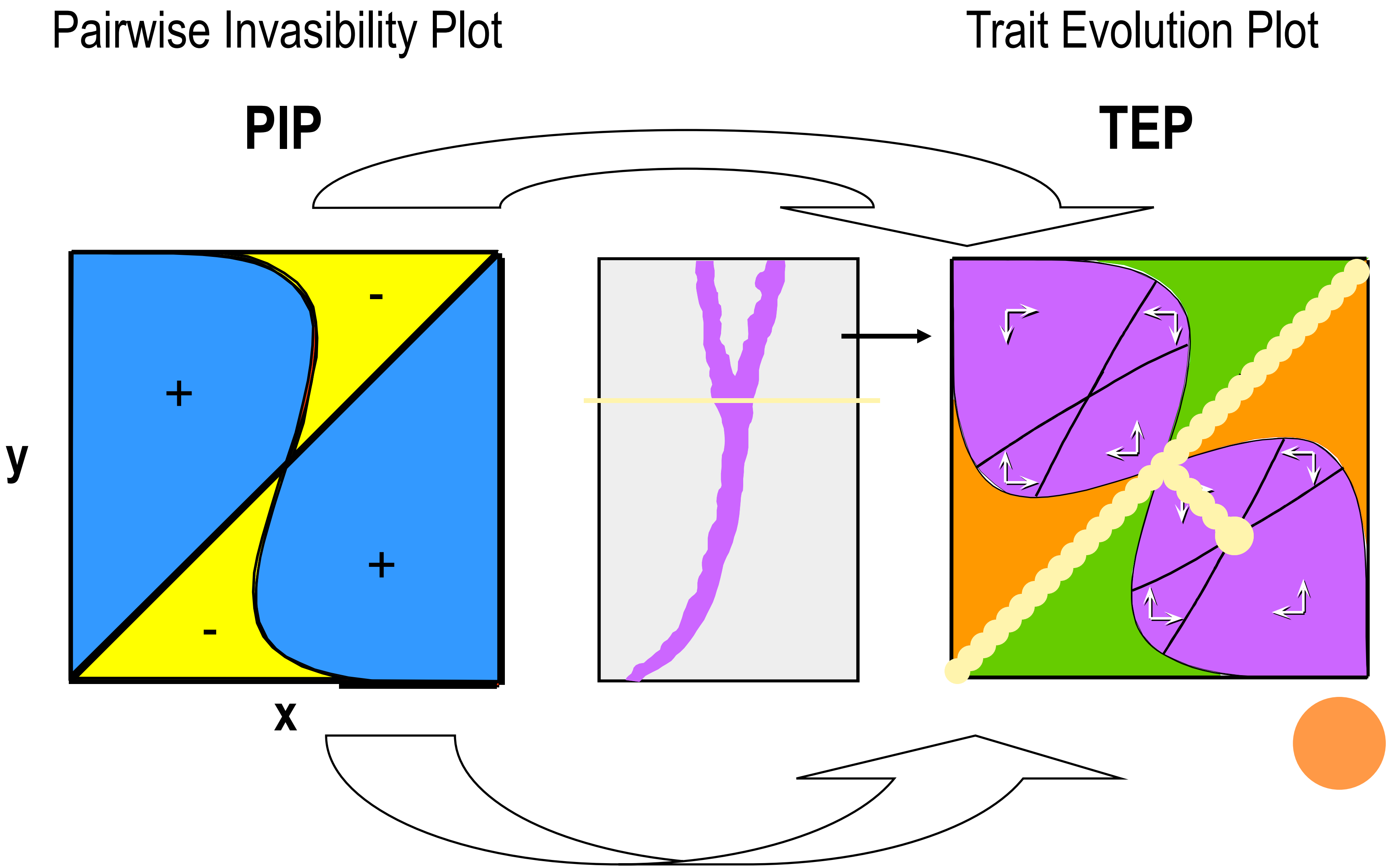

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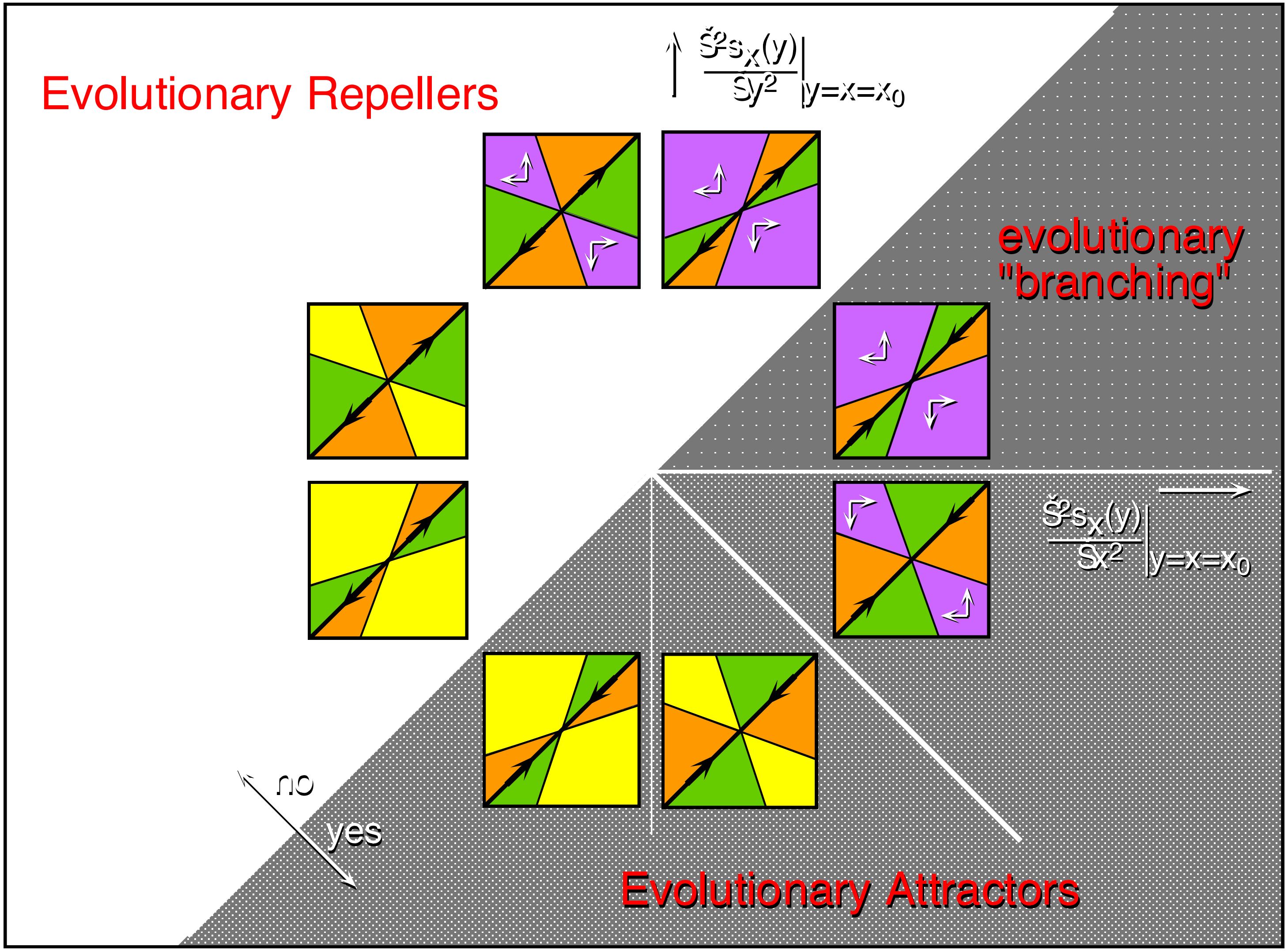

# DIMORPHIC EVOLUTION

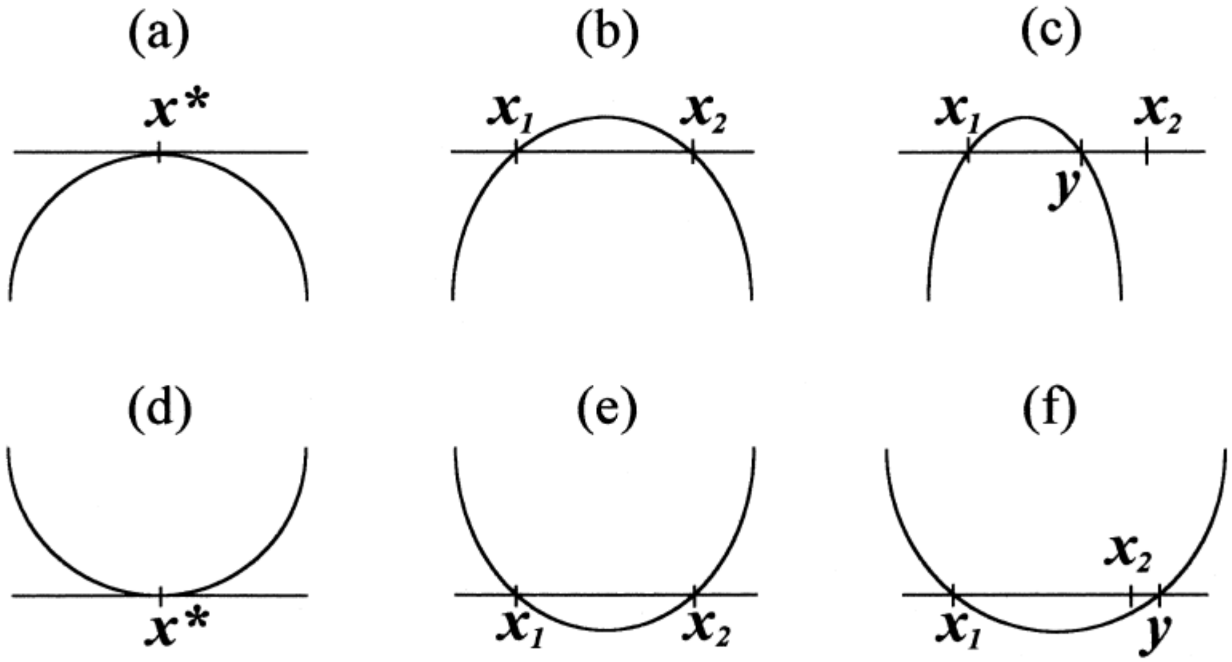


Figure 4. A mutant's fitness in a dimorphic population with strategies $x_1$ and $x_2$ as a perturbation from the fitness in a monomorphic population with a single strategy $x^*$ that is an ESS (a–c) or not an ESS (d–f).

# THE CANONICAL EQUATION (V 2)

- *Structured populations*
- The speed of directional evolution

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

- Durinx and Metz (2005)