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

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OBJECTIF

- Une théorie quantitative pour prédire la *tendance evolutive* (a trajectoire), et les *equilibres* de l’evolution

- Contexte écologique : *fitness* est supposé être déterminé 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

- Monomorphomic vs. polymorphic
  - Monomorphomic = all individuals in the population have the same trait value
  - Polymorphomic = 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 $P_{\text{ext}} = 1$
  - If $r > 0$ then extinction with probability $P_{\text{ext}} < 1$, exponential growth (“invasion”) with probability $(1 - P_{\text{ext}}) > 0$
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)

- 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
    - Fast ecological dynamics
    - Slow 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

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

- Rare mutant of type \( x' \), resident types \( j \) at equilibrium

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

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

\[
f(x', x) = r \left( 1 - a(x', x) \frac{K(x)}{K(x')} \right)
\]
THE CANONICAL EQUATION (V1)

- Unstructured populations
- The speed of directional evolution

\[
\frac{dx}{dt} = \frac{1}{2} \alpha(x) \mu(x) N(x) (\sigma_m(x))^2 \frac{\partial f(x', x)}{\partial x'} \bigg|_{x' = x}
\]
THE COURSE OF EVOLUTION

- Directional selection
  - $\frac{dx}{dt} > 0$ or $<0$

- Evolutionary singular strategies
  - $\frac{dx}{dt} = 0$
  - 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
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
A bit more adaptive dynamics theory for later reference

Pairwise Invasibility Plot

Trait Evolution Plot

PIP

TEP

y

x
A bit more adaptive dynamics theory for later reference

Evolutionary Repellers

Evolutionary Attractors

evolutionary "branching"
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

\[
\frac{d}{dt} X_i \approx \frac{\beta}{T} \frac{\hat{n}_i \mu(X_i)}{\sum_j u_j \text{Var}[\sum_l v_l \xi_{lj}]} \mathbb{M}(X_i) \frac{\partial S_x(X_i)}{\partial Y}^T
\]

- Durinx and Metz (2005)