Adaptation and Evolution

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Overview

1. Modelling Adaptation
2. Challenges in Modelling Adaptation
3. Frameworks for Modelling Adaptation
   a. Evolutionary Games
   b. Adaptive Dynamics
   c. Quantitative Genetics
   d. Evolutionary Algorithms
Modelling Adaptation
System Dynamics

System state

Feedback: Change of state
Types of State Variables

- **Abundances**
  - Nutrient density
  - Number of consumers
  - Capital reserves

- **Properties**
  - Temperature
  - Exploitation strategy
  - Retail price

“Quantities”

“Qualities”
System Dynamics

Abundance dynamics

Abundances

Properties

Property dynamics
Types of Properties

- **Exogenous uncontrollable properties**
  - Resource inflow
  - Disturbance frequency

- **Endogenous uncontrollable properties**
  - Temperature
  - Intensity of competition

- **Endogenous controllable properties**
  - Exploitation strategy
  - Retail price

System parameters

Targets of adaptation
System Dynamics

Growth

Abundances

Uncontrollable properties

Controllable properties

Adaptation
Biological System Dynamics

Ecology

- Abundances
- Environmental properties
- Adaptive traits

Evolution
Targets of Adaptation

- “Endogenous controllable property”
- Strategy
- Behavior
- Response
- Policy

- Character
- Trait
- Phenotype
- Genotype

Too long a name to be useful

Typical for non-biological usage

Typical for biological usage
Types of Adaptive Traits

- Integer-valued: discrete
- Real-valued: scalar, univariate
- Vector-valued: multivariate
- Function-valued: infinite-dimensional
Types of Adaptive Processes

- **Natural selection**: survival of the fittest
- **Imitation**: copy successful behavior
- **Learning**: iteratively refine behavior
- **Deduction**: derive optimal behavior

Increasing cognitive demand
Natural Selection

- Phenotypes that survive longer and/or reproduce more will spread:

![Diagram showing phenotypes spread through generations.](image)
Imitation

Strategies that copy successful behavior will spread:
Learning

- Strategies that iteratively arrive at successful behavior will spread:
Deduction

- Strategies that can derive optimal behavior will spread:
Dawkins’s Replicator Concept

Any entity capable of

- reproduction,
- inheritance of traits allowing for variability, and
- interaction causing reproduction or survival to be trait-dependent

is called a replicator and inevitably will undergo evolution by natural selection.
2 Challenges in Modelling Adaptation
Envisaging evolution as a hill-climbing process on a static fitness landscape is attractively simple, but essentially wrong for most systems.
Describing evolution at the level of phenotypes alone is sometimes not possible.
Genetic Details

- Diploid organisms have two sets of genes, one from the mother, the other from the father.
- Genes can interact with each other nonlinearly, resulting in dominance and epistasis.
- Genes are not all inherited independently, but are typically passed along together with others situated on the same chromosome.
- Also the sex of organisms is determined by two sets of genes (in humans: XX = female, XY = male).
Complication 2:

Frequency-Dependent Selection

Fitness landscapes change in dependence on a population’s current composition.
Eco-Evolutionary Feedback

- Residents
- Variants
- Environment

invade

determine

experience
Complication 3:

Search Space Dimension

Fitness landscapes can be very high dimensional, with topologies that greatly differ from those expected in two or three dimensions.
On high-dimensional fitness landscapes, local peaks in one dimension tend to be connected by a ridge in another dimension.
Historical Developments

1. Population Genetics (1930)
2. Evolutionary Games (1970)
3. Evolutionary Algorithms (1985)

- Quantitative Genetics (1940)
- Adaptive Dynamics (1990)
- Theory of Fitness Landscapes (1995)
Evolutionary Games
Evolutionary games are often based on **discrete strategies** and on **pairwise interactions**.

Pairwise interactions result in **payoffs** that depend on the strategies chosen by the interacting players.

The payoff values are compiled in a **payoff matrix** and define the evolutionary game:

<table>
<thead>
<tr>
<th>If I play…</th>
<th>… and my opponent plays…</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>$W_{AA}$</td>
<td>$W_{AB}$</td>
</tr>
<tr>
<td>$W_{BA}$</td>
<td>$W_{BB}$</td>
</tr>
</tbody>
</table>
Hawk-Dove Game

- A hawk (H) strategist fights for a resource.
- A dove (D) strategist yields to a hawk and shares with a dove, both without fighting.
- Getting the resource confers a benefit $b$ and losing fights implies a cost $c$.

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<thead>
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<th>If I play…</th>
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</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>D</td>
</tr>
</tbody>
</table>

... I receive this payoff:

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>$b/2 - c/2$</td>
<td>$b$</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>$b/2$</td>
</tr>
</tbody>
</table>
Average Payoffs

- **Assumptions:** Populations are large, and individuals encounter each other at random.

- If strategies A and B have abundances $n_A$ and $n_B$, their average payoffs are then given by $W_{AA} n_A + W_{AB} n_B$ and $W_{BA} n_A + W_{BB} n_B$, respectively.

- Using the matrix $W$ and the vector $n = (n_A, n_B)$, we see that these expressions are simply the first and second entry of $Wn$:

$$
Wn = \begin{pmatrix}
W_{AA} & W_{AB} \\
W_{BA} & W_{BB}
\end{pmatrix}
\begin{pmatrix}
n_A \\
n_B
\end{pmatrix}
= 
\begin{pmatrix}
W_{AA} n_A + W_{AB} n_B \\
W_{BA} n_A + W_{BB} n_B
\end{pmatrix}
$$
Assumption: The abundances $n_i$ of strategies $i = A, B, \ldots$ increase according to their average payoffs:

$$\frac{d}{dt} n_i = (Wn)_i$$

Their relative frequencies $p_i$ then always follow the replicator equation:

$$\frac{d}{dt} p_i = (Wp)_i - p \cdot Wp$$

Average payoff in entire population
Replicator Dynamics in the Hawk-Dove Game

- If the cost is smaller than the benefit, $c < b$:
  \[ p_H = 1 \]
  \[ H \]

- If the cost is larger than the benefit, $c > b$:
  \[ p_H = \frac{b}{c} \]
  \[ H \]

Here, a mixed strategy results.
Adaptive Dynamics
Adaptive Dynamics

Adaptive dynamics theory extends evolutionary game theory in a number of respects:

- Density-dependent selection
- Stochastic and nonlinear population dynamics
- Continuous strategies
- Evolutionary dynamics including mutations
- Derivation of fitness function
Invasion Fitness

Definition

Initial per capita growth rate of a small mutant population within a resident population at ecological equilibrium.
Pairwise Invasibility Plots

+ Invasion of the mutant into the resident population possible
- Invasion impossible

One trait substitution

Singular phenotype
Comparison with Recursions

- **Recursion relations**
  - Current state
  - Next state
  - Size of vertical steps deterministic

- **Trait substitutions**
  - Resident trait
  - Mutant trait
  - Size of vertical steps stochastic
Two Interesting Types of PIP

- **Garden of Eden**
- **Branching Point**
Evolutionary Branching

Convergence to disruptive selection leads to endogenous creation of diversity
Assumptions: Populations are large, and mutational steps are both rare and small.

Then the evolutionary rates are given by

\[
\frac{d}{dt} x_i = \frac{1}{2} \mu_i(x_i) n_i^*(x) \sigma_i^2(x_i) \frac{\partial}{\partial x'_i} f_i(x'_i, x) \Big|_{x'_i = x_i}
\]
Quantitative Genetics
Dynamics of Trait Distributions

- Models of quantitative genetics describe evolution in polymorphic populations:

$$\frac{d}{dt} p_i(x_i) = f_i(x_i, p)p_i(x_i) + \frac{1}{2} \mu_i(x_i)\sigma_i^2(x_i) \frac{\partial}{\partial x_i} b_i(x_i, p)p_i(x_i)$$

- Examples are reaction-diffusion dynamics:

**Reaction dynamics**

**Diffusion dynamics**
Problem: Moment Hierarchy

- **0\(^{th}\) moments: Total population densities**
  \[
  \frac{d}{dt} n_i = \ldots n \ldots x \ldots \sigma^2 \ldots
  \]

- **1\(^{st}\) moments: Mean traits**
  \[
  \frac{d}{dt} x_i = \ldots n \ldots x \ldots \sigma^2 \ldots
  \]

- **2\(^{nd}\) moments: Trait variances and covariances**
  \[
  \frac{d}{dt} \sigma_i^2 = \ldots n \ldots x \ldots \sigma^2 \ldots \text{ skewness}
  \]
Lande’s Equation

- **Assumptions:** Populations are large, and total population densities, variances, and covariances are all fixed.

- Then the rates of change in mean trait values are given by

\[
\frac{d}{dt} x_i = \sigma_i^2 \frac{\partial}{\partial x_i} f_i(x'_i, x, n, \sigma^2) \bigg|_{x'_i = x_i}
\]

- Rate of mean trait in species \( i \)
- Current population variance-covariance
- Local selection gradient
- Fitness
Evolutionary Algorithms
Evolutionary algorithms are population-based heuristic optimization tools inspired by biological evolution.

Evolutionary algorithms are not meant to describe real-world systems, but instead aim at solving complex engineering problems.

Solutions are usually not optimal, but good enough for practical purposes.

Some widespread classes of evolutionary algorithms:
- Genetic algorithms
- Genetic programming
- Artificial life (ALife) simulations
- Evolving neural networks
Traveling Salesman Problem

- **Goal:** Find shortest path through a collection of cities.

- **Approach:** Consider sequence of cities as genotypes, mutate by permuting city pairs, and reproduce with fitness given by inverse path length.
Pole Balancing Problem

- **Goal:** By moving a cart, bring hinged pole upright and keep cart centered.

- **Approach:** Describe neural network controllers as genotypes, mutate by adding or removing neurons and links or by changing link weights, reproduce with performance-based fitness.
Adaptation is ubiquitous in all systems involving humans or other organisms.

Adaptation can be based on natural selection or on more advanced cognitive mechanisms like imitation, learning, or deduction.

Excluding the possibility of adaptation from models can result in serious mispredictions.

Mutually complementary tools for studying adaptation are provided by evolutionary games, adaptive dynamics, quantitative genetics, and evolutionary algorithms.