The Mathematical Interaction of “Flop” and “Wear-and-Tear” (Morin, 2011)

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A GENERALIZATION OF THEORY

ON THE EVOLUTION OF MODIFIER GENES

By
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A DISSERTATION

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

(3) A MODEL FOR MODIFIERS IN CULTURAL TRANSMISSION
A General Framework for Evolutionary Dynamics

- **Basic population and evolutionary dynamical elements:**
  1. Growth
  2. Transformation of information (changes of state)
  3. Finite sampling
Fundamental Processes: (1) Growth

GROWTH

DECAY (NEGATIVE GROWTH)

MATHEMATICAL FORMS e.g.:

\[ x(t+1) = \lambda x(t) \]

\[ \frac{dx(t)}{dt} = \lambda x(t) \]
**Fundamental Processes: (2) Transformation**

**TRANSFORMATION (i.e. CHANGE OF STATE)**

**MATHEMATICAL FORMS e.g.:**

\[ x(t+1) = \sum_y P_{xy} y(t) \]

\[ \frac{\partial}{\partial t} u(x, t) = \Delta u(x, t) \]
Growth and Transformation Combined

**GROWTH + TRANSFORMATION**

MATHEMATICAL FORMS e.g.:

\[
x(t+1) = \sum_y P_{xy} \lambda_y y(t)
\]

\[
\frac{\partial}{\partial t} u(x, t) = \Delta_x u(x, t) + \lambda(u) u(x, t)
\]
**Growth and Transformation are Ubiquitous**

<table>
<thead>
<tr>
<th>Objects</th>
<th>Transformation /Mixing between:</th>
<th>Heterogeneous growth/decay rates:</th>
</tr>
</thead>
<tbody>
<tr>
<td>genomes</td>
<td>genotypes</td>
<td>fitnesses</td>
</tr>
<tr>
<td>organisms</td>
<td>locations</td>
<td>survival &amp; replication rates</td>
</tr>
<tr>
<td>microbes</td>
<td>tissue compartments</td>
<td>survival &amp; replication rates</td>
</tr>
<tr>
<td>metabolites</td>
<td>tissue compartments</td>
<td>catabolic rates</td>
</tr>
<tr>
<td>reactants</td>
<td>diffusion of position</td>
<td>reaction &amp; decay rates</td>
</tr>
<tr>
<td>wastes</td>
<td>reactor sites</td>
<td>breakdown rates</td>
</tr>
<tr>
<td>culture</td>
<td>content</td>
<td>transmission &amp; adoption rates</td>
</tr>
<tr>
<td>capital</td>
<td>investments</td>
<td>rates of return</td>
</tr>
<tr>
<td>photons</td>
<td>transmitting media</td>
<td>absorption rates</td>
</tr>
<tr>
<td>particles</td>
<td>interacting matter</td>
<td>reaction &amp; decay rates</td>
</tr>
</tbody>
</table>
**Q.** How can we possibly understand the interaction of complex transmission with different growth rates over multiple generations?

**A.** Spectral theory.

**MATHEMATICAL FORMS e.g.:**

\[ x(t+1) = \sum_{y} P_{xy} \lambda_{y} y(t) \]

\[ \frac{\partial}{\partial t} u(x, t) = \Delta_{x} u(x, t) + \lambda(u) u(x, t) \]
Spectral Theory

\[
D_1 = 2.0 \\
D_2 = 0.5
\]

\[
\begin{align*}
M &= \begin{bmatrix} 1 - p_{21} & p_{12} \\ p_{21} & 1 - p_{12} \end{bmatrix}, \\
D &= \begin{bmatrix} 2.0 & 0 \\ 0 & 0.5 \end{bmatrix}
\end{align*}
\]

\[
\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \end{bmatrix} = \begin{bmatrix} 1 - p_{21} & p_{12} \\ p_{21} & 1 - p_{12} \end{bmatrix} \begin{bmatrix} 2.0 & 0 \\ 0 & 0.5 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}
\]

\[
x(t) = (M D)^t x(0)
\]
For any initial frequencies $x(0)$, in the limit of large time,

$$\lim_{t \to \infty} x(t) = \lim_{t \to \infty} (MD)^t x(0) = r^t \hat{x},$$

where
- $r$ is the largest eigenvalue of $MD$, and
- $\hat{x}$ is its associated eigenvector.

If $r < 1$ then $\lim_{t \to \infty} x(t) = 0$.

i.e. $x$ is a “flop”. 
Eigenvectors: The hidden “modules” of matrices. Here is a matrix chosen out of the hat:

\[
\begin{bmatrix}
0.624 & 0.563 & 0.498 \\
0.172 & 0.036 & 0.611 \\
0.005 & 0.362 & 0.569
\end{bmatrix}.
\]

Let’s multiply it by a vector:

\[
\begin{bmatrix}
0.624 & 0.563 & 0.498 \\
0.172 & 0.036 & 0.611 \\
0.005 & 0.362 & 0.569
\end{bmatrix} \cdot \begin{bmatrix} 1/3 \\ 1/3 \\ 1/3 \end{bmatrix} =
\begin{bmatrix}
0.624 \times 1/3 + 0.563 \times 1/3 + 0.498 \times 1/3 \\
0.172 \times 1/3 + 0.036 \times 1/3 + 0.611 \times 1/3 \\
0.005 \times 1/3 + 0.362 \times 1/3 + 0.569 \times 1/3
\end{bmatrix} =
\begin{bmatrix}
0.561 \\
0.273 \\
0.312
\end{bmatrix}.
Eigenvector and Eigenvalue #1

There are **exactly 3 vectors** that “pass through” the matrix as though the matrix was a single number.

These **eigenvectors** are the component **“colors”** of the matrix — it’s spectrum.

\[
\begin{bmatrix}
0.624 & 0.563 & 0.498 \\
0.172 & 0.036 & 0.611 \\
0.005 & 0.362 & 0.569
\end{bmatrix} \bullet \begin{bmatrix} 0.891 \\ 0.344 \\ 0.296 \end{bmatrix}
\]

\[
= \begin{bmatrix}
0.624 \times 0.891 + 0.563 \times 0.344 + 0.498 \times 0.296 \\
0.172 \times 0.891 + 0.036 \times 0.344 + 0.611 \times 0.296 \\
0.005 \times 0.891 + 0.362 \times 0.344 + 0.569 \times 0.296
\end{bmatrix}
\]

\[
= 1.006709 \times \begin{bmatrix} 0.891 \\ 0.344 \\ 0.296 \end{bmatrix}
\]
Eigenvector and Eigenvalue #2

\[
\begin{bmatrix}
0.624 & 0.563 & 0.498 \\
0.172 & 0.036 & 0.611 \\
0.005 & 0.362 & 0.569
\end{bmatrix}
\cdot
\begin{bmatrix}
-0.967 \\
-0.027 \\
0.252
\end{bmatrix}
= 0.5096893 \times
\begin{bmatrix}
-0.967 \\
-0.027 \\
0.252
\end{bmatrix}
\]
Eigenvector and Eigenvalue #3

\[
\begin{bmatrix}
0.624 & 0.563 & 0.498 \\
0.172 & 0.036 & 0.611 \\
0.005 & 0.362 & 0.569
\end{bmatrix} \bullet \begin{bmatrix}
0.337 \\
-0.868 \\
0.365
\end{bmatrix}
\]

\[
\begin{bmatrix}
0.624 \times 0.337 + 0.563 \times (-0.868) + 0.498 \times 0.365 \\
0.172 \times 0.337 + 0.036 \times (-0.868) + 0.611 \times 0.365 \\
0.005 \times 0.337 + 0.362 \times (-0.868) + 0.569 \times 0.365
\end{bmatrix}
\]

\[
= -0.2873466 \times \begin{bmatrix}
0.337 \\
-0.868 \\
0.365
\end{bmatrix}
\]
Almost all $n \times n$ matrices have $n$ such eigenvectors, each with its own eigenvalue.

When we keep multiplying a matrix, the result

$$\lim_{t \to \infty} x(t) = \lim_{t \to \infty} (M D)^t x(0) = r^t \hat{x},$$

becomes dominated by the eigenvector with the largest eigenvalue, the spectral radius.

If $r < 1$ then $\lim_{t \to \infty} x(t) = 0$, i.e. $x$ is a “flop”.

If $r \geq 1$ then $\lim_{t \to \infty} x(t) > 0$, i.e. $x$ survives.
An Example: Transmission of Children’s Games

"Jeunestat"

Feed

Effluent
“Wear-and-Tear” Graph of a Tradition

The network of versions of a tradition due to imperfect transmission.
The graph illustrates the proliferation rate of versions of a tradition, sorted into "Hit" and "Flop" categories. The x-axis represents the versions of the tradition, sorted, while the y-axis shows the proliferation rate. The "Hit" versions show a higher proliferation rate compared to the "Flop" versions.
Each time the tradition is transmitted:

- With probability $m$ it undergoes “wear-and-tear”;
- With probability $1 - m$ it is transmitted unchanged.

How big can $m$ be and the tradition still proliferates?

\[ m^* = 0.572 \]
The Reduction Principle
Feldman (1972) discovered a “Reduction Principle” in models for the evolution of recombination, mutation, and dispersal rates: they each would evolve downward in populations near equilibrium.

For my dissertation, I unified these results using the following fundamental theorem of Sam Karlin:

**Theorem (Karlin’s Theorem 5.2, (1982))**

Let $\mathbf{M}$ be a non-negative irreducible stochastic matrix. Consider the family of matrices

$$
\mathbf{M}(\alpha) = (1-\alpha)\mathbf{I} + \alpha \mathbf{M}, \quad 0 \leq \alpha \leq 1.
$$

Then for any positive diagonal matrix $\mathbf{D}$, the spectral radius

$$
r(\alpha) = r(\mathbf{M}(\alpha)\mathbf{D})
$$

is decreasing as $\alpha$ increases (strictly provided $\mathbf{D} \neq d\mathbf{I}$).
Karlin’s Intuition: *Mixing reduces growth and hastens decay*

Something everyone kinda knows:
Illustration of Karlin’s Theorem 5.2, cont’d

\[ D_1 = 2.0 \]
\[ D_2 = 0.5 \]

\[
MD = \begin{bmatrix}
1 - p_{21} & p_{12} \\
p_{21} & 1 - p_{12}
\end{bmatrix}
\begin{bmatrix}
2.0 \\
0
\end{bmatrix}
\begin{bmatrix}
0 \\
0.5
\end{bmatrix}
\]
Illustation of Karlin’s Theorem 5.2, cont’d

Karlin’s Theorem 5.2: Spectral Radius increases along each line to (0,0)

$D_1 = 2.0$

$D_2 = 0.5$
The Reduction Principle: populations at a balance between transmission and natural selection will evolve to reduce the rate of error in transmission.

Fundamental implication: evolution has two different properties that it operates to maximize:

1. organismal fitness, and

2. the fidelity of information transmission.
Suppose there is a tradeoff between fitness and fidelity:

<table>
<thead>
<tr>
<th></th>
<th>Fitness Version A</th>
<th>Fitness Version B</th>
<th>Transformation Rate $p_{12} = p_{21}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tradition 1</td>
<td>8</td>
<td>2</td>
<td>0.2</td>
</tr>
<tr>
<td>Tradition 2</td>
<td>6.7</td>
<td>1</td>
<td>0.02</td>
</tr>
</tbody>
</table>

- So, ** Tradition 1 dominates Tradition 2** in its fitnesses in both Version A and Version B.
- It’s obvious that Tradition 1 will outcompete Tradition 2, right?
\[ \mathbf{MD} = \begin{bmatrix} 0.8 & 0.2 & 0 & 0 \\ 0.2 & 0.8 & 0 & 0 \\ 0 & 0 & 0.98 & 0.02 \\ 0 & 0 & 0.02 & 0.98 \end{bmatrix} \times \text{diag} \begin{bmatrix} 8 \\ 2 \\ 6.7 \\ 1 \end{bmatrix}. \]

Stationary distribution:

\[
\lim_{t \to \infty} \frac{1}{r(\mathbf{MD})^t} (\mathbf{MD})^t \mathbf{x}(0) = c \begin{bmatrix} 0 \\ 0 \\ 0.9964 \\ 0.0036 \end{bmatrix}.
\]

- Tradition 2 \((r = 6.57)\) beats Tradition 1 \((r = 6.53)\) even though Tradition 1’s fitnesses \(\{8, 2\}\) dominate Tradition 2’s fitnesses \(\{6.7, 1\}\)
- because Tradition 2 has lower mixing \((0.02 \text{ vs. } 0.20)\).
Pop Gen vs. EvoDevo

1. The *fate of variation*: The main concern of classical population genetics

2. The *generation of variation*: A central concern of evo-devo and the “extended synthesis”

3. My focus: Examine the *fate of variation for the generation of variation*. 
Mendelian Diploid Genetics:

\[ G_{j1} \rightarrow G_{j2} \rightarrow G_{j3} \rightarrow \ldots \rightarrow G_{jn} \]

\[ G_{k1} \rightarrow G_{k2} \rightarrow G_{k3} \rightarrow \ldots \rightarrow G_{kn} \]

\[ T(i \leftarrow j, k) \]

\[ G_{i1} \rightarrow G_{i2} \rightarrow G_{i3} \rightarrow \ldots \rightarrow G_{in} \]
Nei’s (?) Modifier Gene Model (Generalized)

\[
\begin{align*}
M_a &\quad G_{j_1} & G_{j_2} & G_{j_3} & \cdots & G_{j_n} \\
M_b &\quad G_{k_1} & G_{k_2} & G_{k_3} & \cdots & G_{k_n} \\
\end{align*}
\]

\[G_j \quad r \quad G_k\]

controlled by \(M_a \cdot M_b\)

\[T_{ab}(i \leftarrow j, k)\]
Fidelity Variation Model

TOMAYTO    TOMAHTO  ➔  TOMARTO

[Image of silhouettes of a man and a woman toasting, a child pointing]
Differential Fitness:
Random Mating:
Fidelity Variation Model (A., 1984)

- Individuals bear two kinds of culturally transmitted traits. They determine:
  1. Fitness: Viability of its bearer and fertility of the couple.
  2. Fidelity: The fidelity of transmission of the fitness-determining trait.

- Offspring are produced from two parents. Offspring randomly choose one of their parents with whom they will “identify”.

- The offspring acquire from the parent with whom they identify their degree of fidelity.

- This fidelity determines the probability that they also acquire the same selected cultural trait as the parent with whom they identify. Otherwise, they acquire a selected trait which is some function of the selected traits in both their parents.
Fidelity Variation Model

Mathematical representation of the model:

\( x_{ai} \) Frequency of individuals with fidelity type \( a \) and selected type \( i \) before selection.

\( w_{ij} \) Lumped viability and fertility of parental pairs with selected types \( i \) and \( j \).

\( 1 - m_a \) Probability that an offspring adopts the selected trait of the parent with whom it identifies.

\( T(i \leftarrow j, k) \) Probability that an offspring of parental selected types \( j \) and \( k \) is of selected type \( i \) given that it does not simply copy the parent with whom it identifies.
Fidelity Variation Model

For a life cycle consisting of selection, random mating with fertility selection, and cultural transmission, the recursion on the frequencies of types is

\[ x_{ai}(t+1) = \sum_{bjk} x_{aj}(t) x_{bk}(t) \frac{w_{jk}}{\bar{w}} [(1 - m_a) \delta_{ji} + m_a T(i \leftarrow j, k)] \]

or in vector form

\[ \mathbf{x}_a(t+1) = [(1 - m_a) \mathbf{I} + m_a \mathbf{P}(t)] \mathbf{D}(t) \mathbf{x}_a(t), \]

where \( v_k(t) = \sum_a x_{ak}(t), \ w_j(t) = \sum_k v_k(t) w_{jk}, \)

\[ \mathbf{P}(t) = \left[ \sum_k v_k(t) \frac{w_{jk}}{w_j(t)} T(i \leftarrow j, k) \right]_{i,j}, \quad \bar{w}(t) = \sum_{jk} v_j(t) v_k(t) w_{jk}, \quad \text{and} \]

\[ \mathbf{D} = \frac{1}{\bar{w}(t)} \text{diag} [w_j(t)]. \]
Fidelity Variation Model, concluded

The long-term growth rate of fidelity type \( a \) is the largest eigenvalue of \([ (1 - m_a)I + m_a P ] D\),

\[ r([ (1 - m_a)I + m_a P ] D). \]

Karlin’s Theorem 5.2 yields this immediate result:

**Result**

*The population fixes on the highest degree of fidelity in the population (the lowest \( m_a \)).*

- This is just one example in which the “reduction phenomenon” manifests itself.
- It is a fundamental property of the interaction of mixing processes with different rates of growth.
- This is just the tip of the iceberg of the properties that emerge from the interaction of “flop” and “wear-and-tear”. 
Thank you for your kind attention.

Bon Voyage Mathieu!
References


