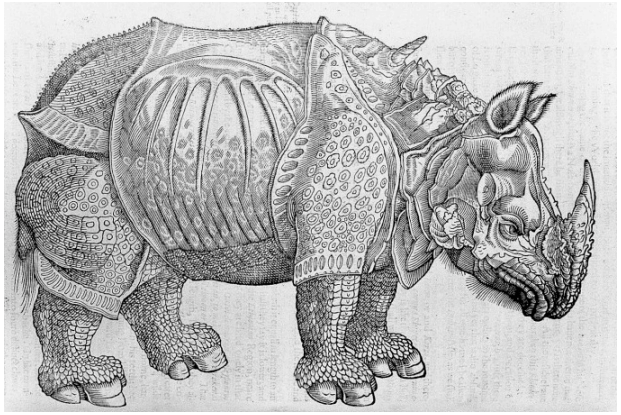
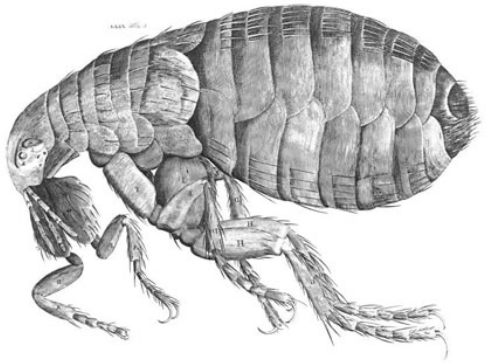
Evolutionary Theory



Foundations



David Krakauer, Santa Fe Institute.

(please do not reproduce without permission)

Fundamental Evolutionary questions?

- Why is there life-like dynamics on earth?
- Why are organisms so diverse?
- Why are organisms so complex?
- What is the relationship or organismal to ecological structure?
- What is the relationship of genetic information to learned information?
- When does cultural evolution outpace genetic evolution?
- Is “self-awareness” inevitable?

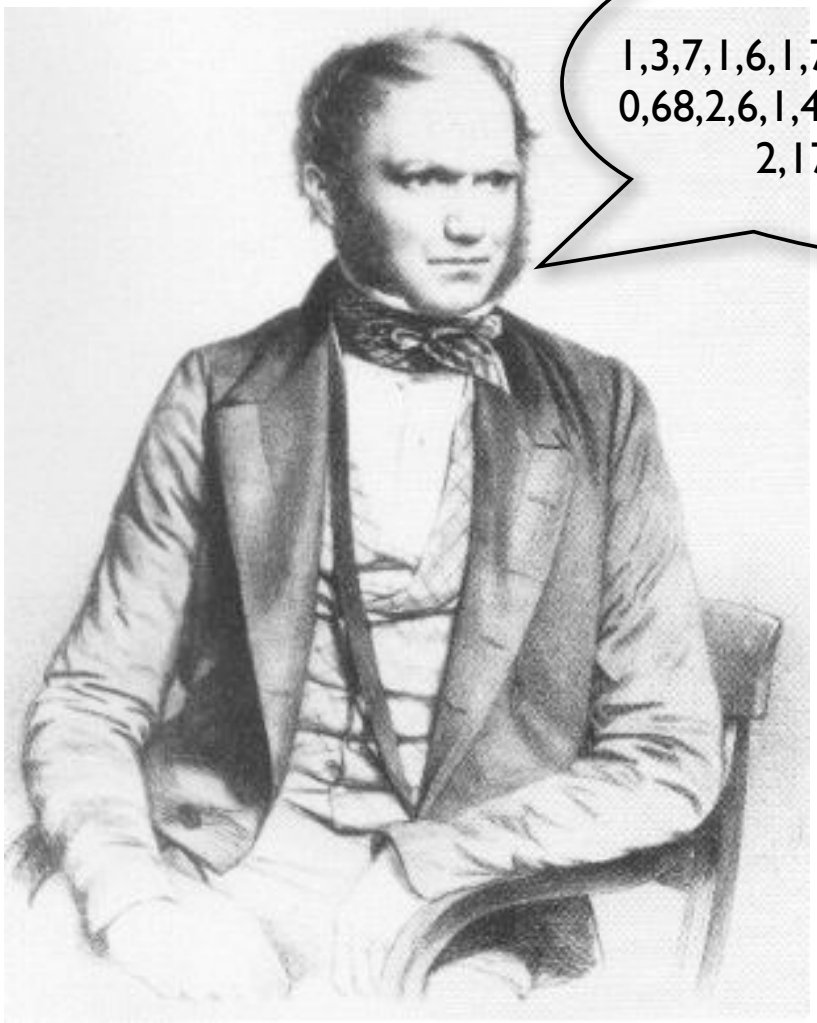
ASTOUNDING SUPER-SCIENCE FANTASIES!
STRANGE WORLDS
10c
No.7
space-gods of planetoid 50
sabotage on space station 1
the man who fought the world

THE ANDROMEDA STRAIN
It's a bad day to be human.
TWO-NIGHT TELEVISION EVENT
A&E
PREMIERES MEMORIAL DAY 9/8C

What is Evolutionary Theory?

- A Physics like theory searching for Laws?
- A Statistical/Inferential Theory like Bayesian learning or approximate dynamic programming?
- An algorithmic/computational theory?
- A narrative, historical description of life on earth structured by a plot called natural selection.

The Darwinian Polynucleotide Machine



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2,176,2,1,1,2 (in MegaBases)

Table 1. A summary of some common misconceptions about evolution and complexity, and contrasting views

Myth	Reality
1. Evolution is natural selection.	Natural selection is just one of four primary evolutionary forces.
2. Characterization of interspecific differences at the molecular and/or cellular levels is tantamount to identifying the mechanisms of evolution.	The resources deployed in evolutionary change reside at the molecular level, but whereas the cataloging of such differences at the interspecific level identifies the end products of evolution, it does not reveal the population-genetic processes that promoted such change.
3. Microevolutionary theory based on gene-frequency change is incapable of explaining the evolution of complex phenotypes.	No principle of population genetics has been overturned by an observation in molecular, cellular, or developmental biology, nor has any novel mechanism of evolution been revealed by such fields.
4. Natural selection promotes the evolution of organismal complexity.	There is no evidence at any level of biological organization that natural selection is a directional force encouraging complexity. In contrast, substantial evidence exists that a reduction in the efficiency of selection drives the evolution of genomic complexity.
5. Natural selection is the only force capable of promoting directional evolution.	Both mutation and gene conversion are nonrandom processes that can drive the patterning of genomic evolution in populations with sufficiently small effective sizes (common in multicellular lineages).
6. Genetic drift is a random process that leads to noise in the evolutionary process, but otherwise leaves expected evolutionary trajectories unaltered.	By reducing the efficiency of selection, random genetic drift imposes a high degree of directionality on evolution by increasing the likelihood of fixation of deleterious mutations and decreasing that of beneficial mutations.
7. Mutation merely creates variation, whereas natural selection promotes specific mutant alleles on the basis of their phenotypic effects.	Mutation operates as a weak selective force by differentially eliminating alleles with structural features that magnify mutational target sizes.
8. Phenotypic and genetic modularity are direct products of natural selection.	There is no evidence that the modular structure of gene regulatory regions or genetic networks is directly advanced by selective mechanisms. However, the processes of duplication, degenerative mutation, and random genetic drift can lead to the passive emergence of modularity in populations of with genetic effective sizes of the magnitude found in multicellular species.
9. Natural selection promotes the ability to evolve.	There is no evidence that phylogenetic variation in the pathways open to evolutionary exploration is anything more than a by-product of physical processes that passively arise with expansions in genome size and generation length. There are no abrupt transitions in aspects of genomic architecture or gene structure between unicellular and multicellular species, nor between viruses, prokaryotes, and eukaryotes.

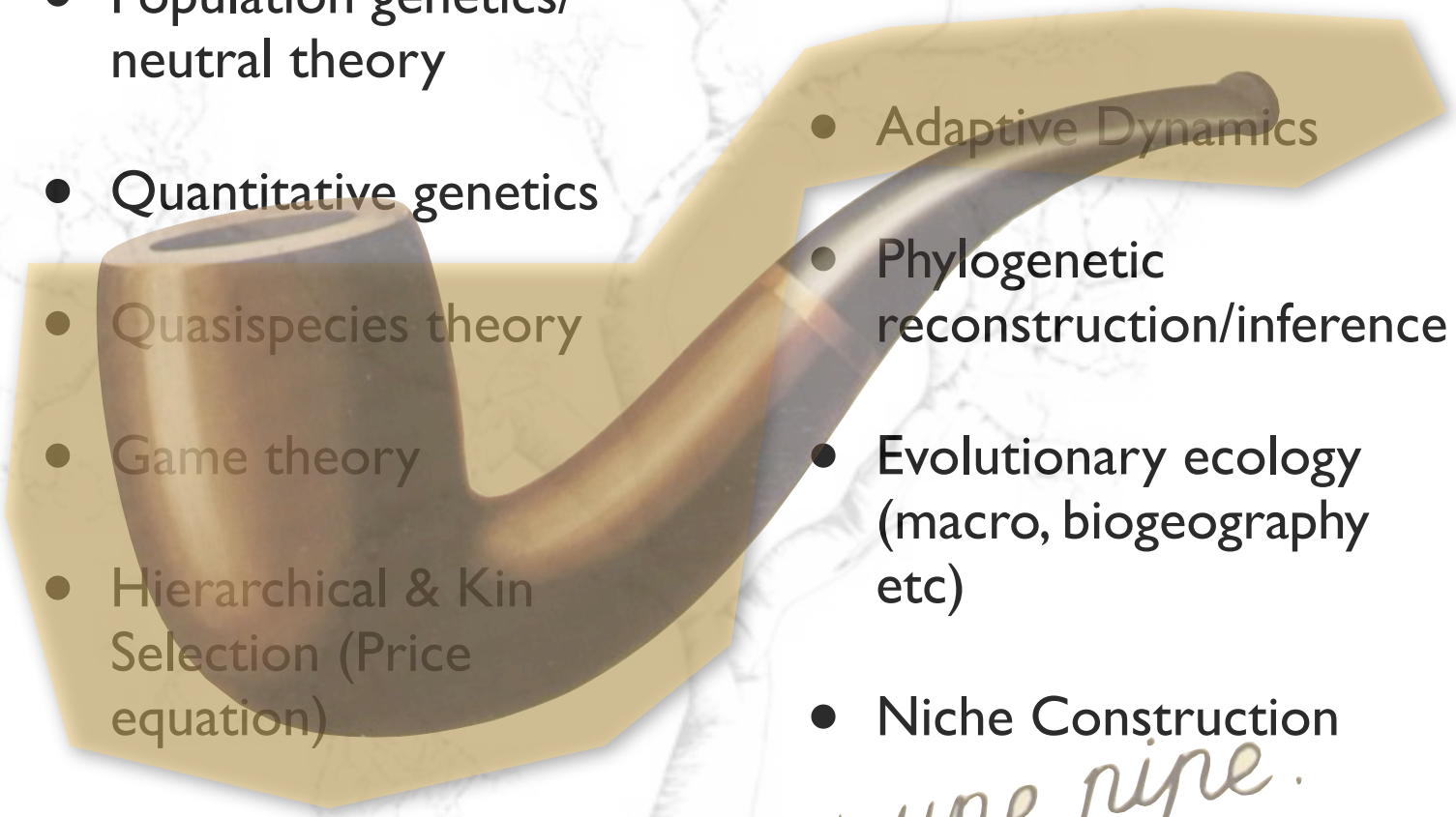
Lynch, PNAS, 104, 8597-8604 2007

Assumptions

- Biochemistry/physiology is capable of *storing* information in compact, localized, & predictive structures (individuality).
- Individuals tend to decay and hence achieve persistence through replication.
- Individuals possess features that are constructed (develop) to promote persistence and decay of self & others (adaptations).
- Individuals are capable of sharing adaptive information (recombination, sex etc).

Evolutionary Theory

- Population genetics/ neutral theory
- Quantitative genetics
- Quasispecies theory
- Game theory
- Hierarchical & Kin Selection (Price equation)
- Adaptive Dynamics
- Phylogenetic reconstruction/inference
- Evolutionary ecology (macro, biogeography etc)
- Niche Construction



Evolutionary Stoichiometry

replication

$$g_i \xrightarrow[\text{Energy} + \text{Resources}]{r_i} 2g_i$$

Evolutionary Stoichiometry

competition

$$g_i + g_j \xrightarrow{c_{ij}} g_j$$

Evolutionary Stoichiometry

mutation

$$g_i \xrightarrow[\text{Radiation}]{m_{ij}} g_j$$

$$m_{ij} = \mu^{H(i,j)}(1-\mu)^{L-H(i,j)}$$

Evolutionary Stoichiometry

recombination

$$g_j + g_l \xrightarrow{b_{ijl}} g_i$$

$$b_{ijl} = 1, \quad \text{if} \quad i = j = l$$

$$b_{ijl} = \left(\frac{1}{2}\right)(1-c) + c\left(\frac{1}{2}\right)^{H(j,l)} \quad \text{if} \quad i = j \quad \text{or} \quad i = l$$

$$b_{ijl} = c\left(\frac{1}{2}\right)^{H(j,l)} \quad \text{if} \quad H(i,j) + H(i,l) = H(j,l)$$

Evolutionary Stoichiometry

Development

$$g_j + g_l \xrightarrow{d_{ijl}} p_i$$

Typically Treated Thus

$$g_i \xrightarrow{d_i} p_i$$

Replicator Equation

$$g_i \xrightarrow{r_i} 2g_i$$

$$g_i + g_j \xrightarrow{c_{ij}} g_j$$

n genomes

$$\dot{g}_i = g_i(r_i - \bar{f})$$

where $\bar{f} = \sum_i^n r_i g_i$ and $c_{ij} = 1$

Evolutionary Game Theory: Frequency dependent Replicator Equation

$$g_i \xrightarrow{r_i(\mathbf{g})} 2g_i$$

$$g_i + g_j \xrightarrow{c_{ij}} g_j$$

n genomes

$$\dot{g}_i = g_i(r_i(\mathbf{g}) - \bar{f})$$

where $\bar{f} = \sum_i^n r_i(\mathbf{g}) g_i$ and $c_{ij} = 1$

Evolutionary Game Theory: Frequency dependent Replicator Equation

$$\dot{g}_i = g_i(r_i(\mathbf{g}) - \bar{f})$$

$$\text{Payoff Matrix } \; P = [p_{ij}]$$

with linear payoffs:

$$r_i(\mathbf{g}) = \sum_j^n g_j p_{ij}$$

Evolutionary Game Theory: Frequency dependent Replicator Equation

$$\dot{g}_i = g_i(\sum_j^n g_j p_{ij} - \sum_j^n g_j \sum_k^n g_k p_{jk})$$

Freq-dep Replicator Equation & Bayesian Inference

An Insight by Cosma Shalizi

$$\frac{\Delta g_i(t)}{\Delta t} = g_i(t-1)(r_i(\mathbf{g}) - \bar{f})$$

$$P(X|Y) = P(X)\frac{P(Y|X)}{P(Y)}$$

$$P(X|Y) = P(X)\frac{L_X}{\bar{L}}$$

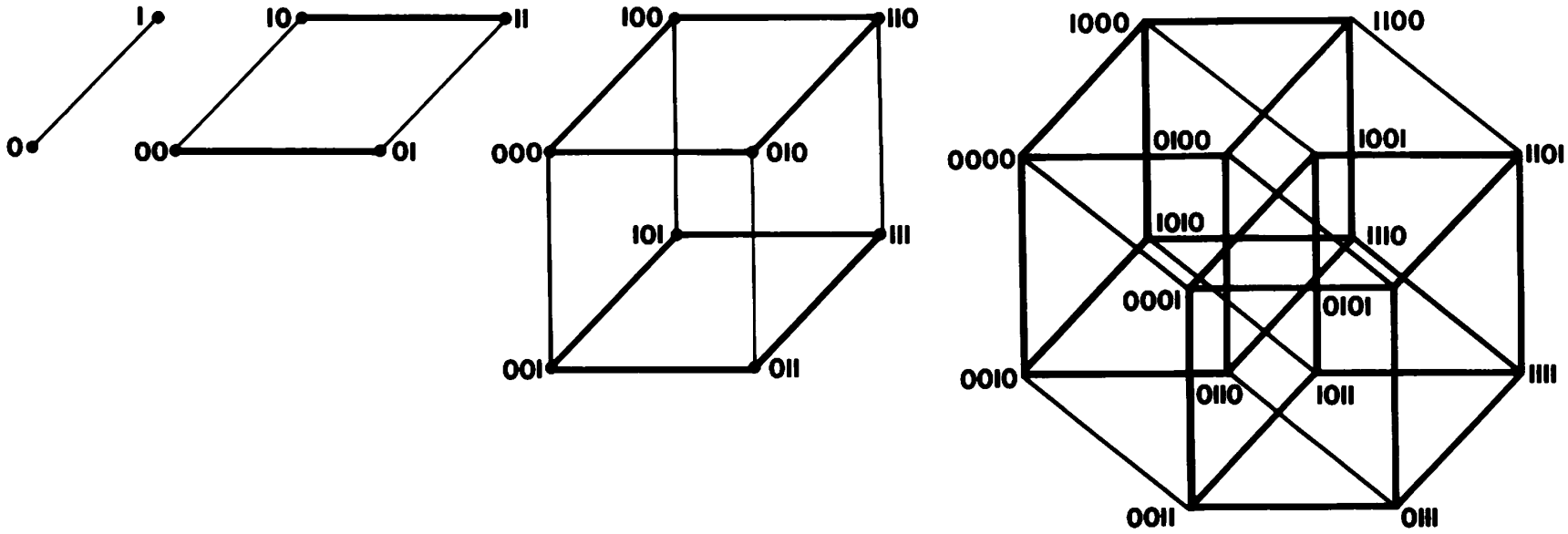
$$\bar{L} = P(Y) = \sum_{x \in \omega} P(Y|X)P(X)$$

$$P_X(t) = P_X(t-1)\frac{L_X}{\bar{L}}$$

$$\Delta P_X(t) = P_X(t-1)(\frac{L_X}{\bar{L}} - 1) = P_X(t-1)\frac{1}{\bar{L}}(L_X - \bar{L})$$

$$\Delta P_X(t) = P_X(t-1)(f_t - \bar{f}), \quad \text{where} \quad f_t = L_X/\bar{L}$$

Mutation & Sequence Space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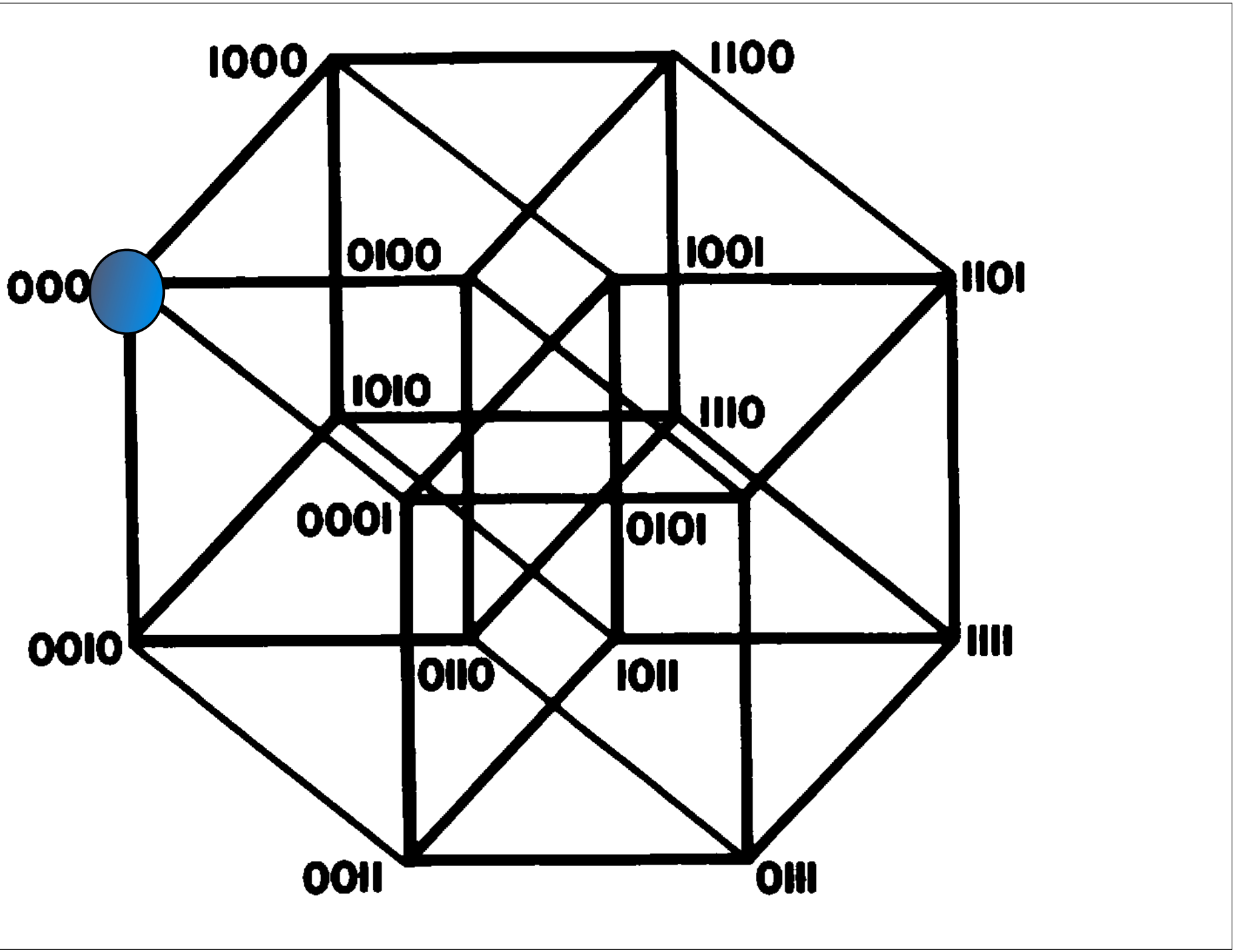
Replicator-Mutator Equation

$$\dot{g}_i = \sum_{j}^{2^n} g_j r_j(\mathbf{g}) m_{ij} - g_i \bar{f})$$

$$m_{ij} = \mu^{H(i,j)} (1-\mu)^{L-H(i,j)}$$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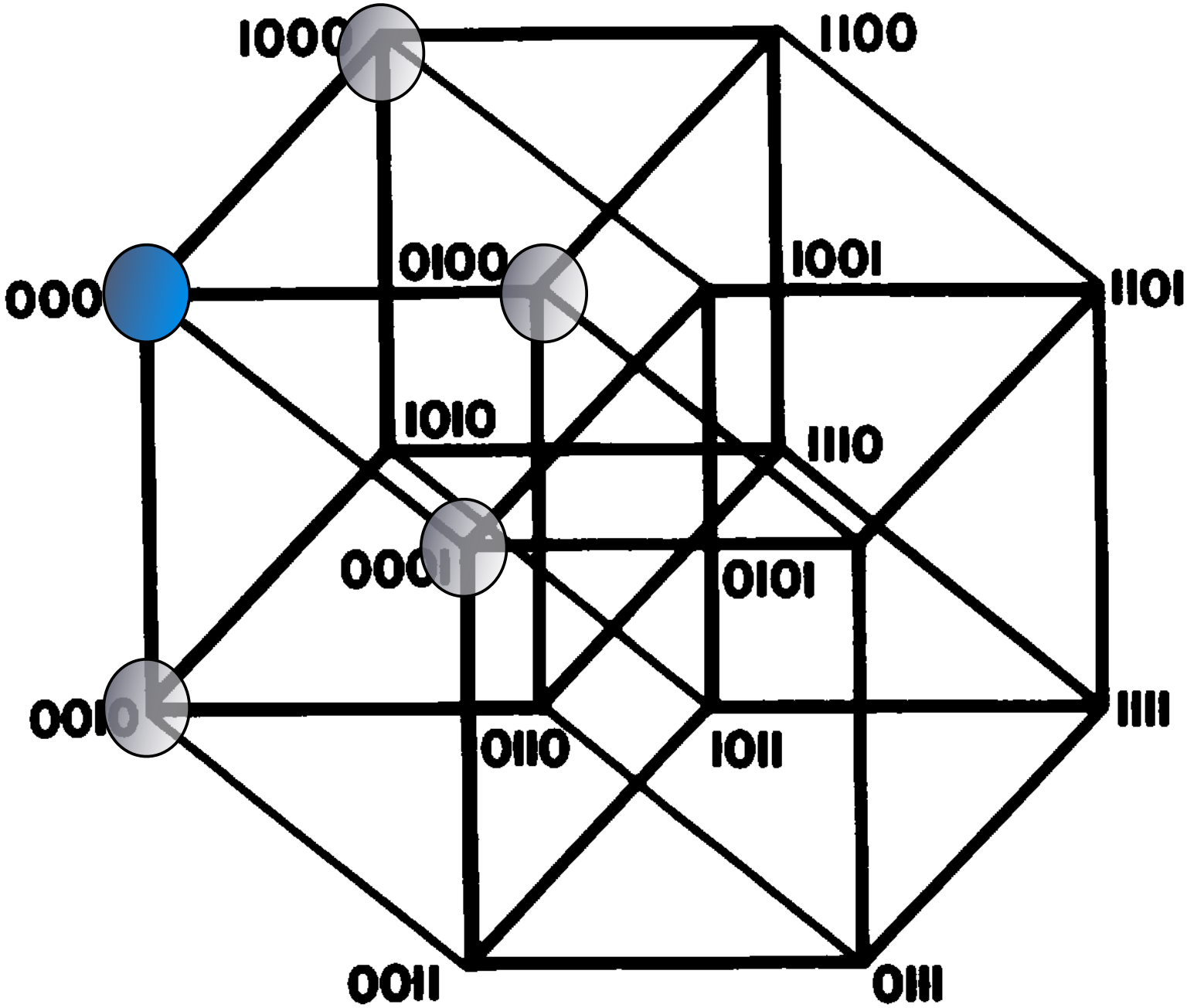
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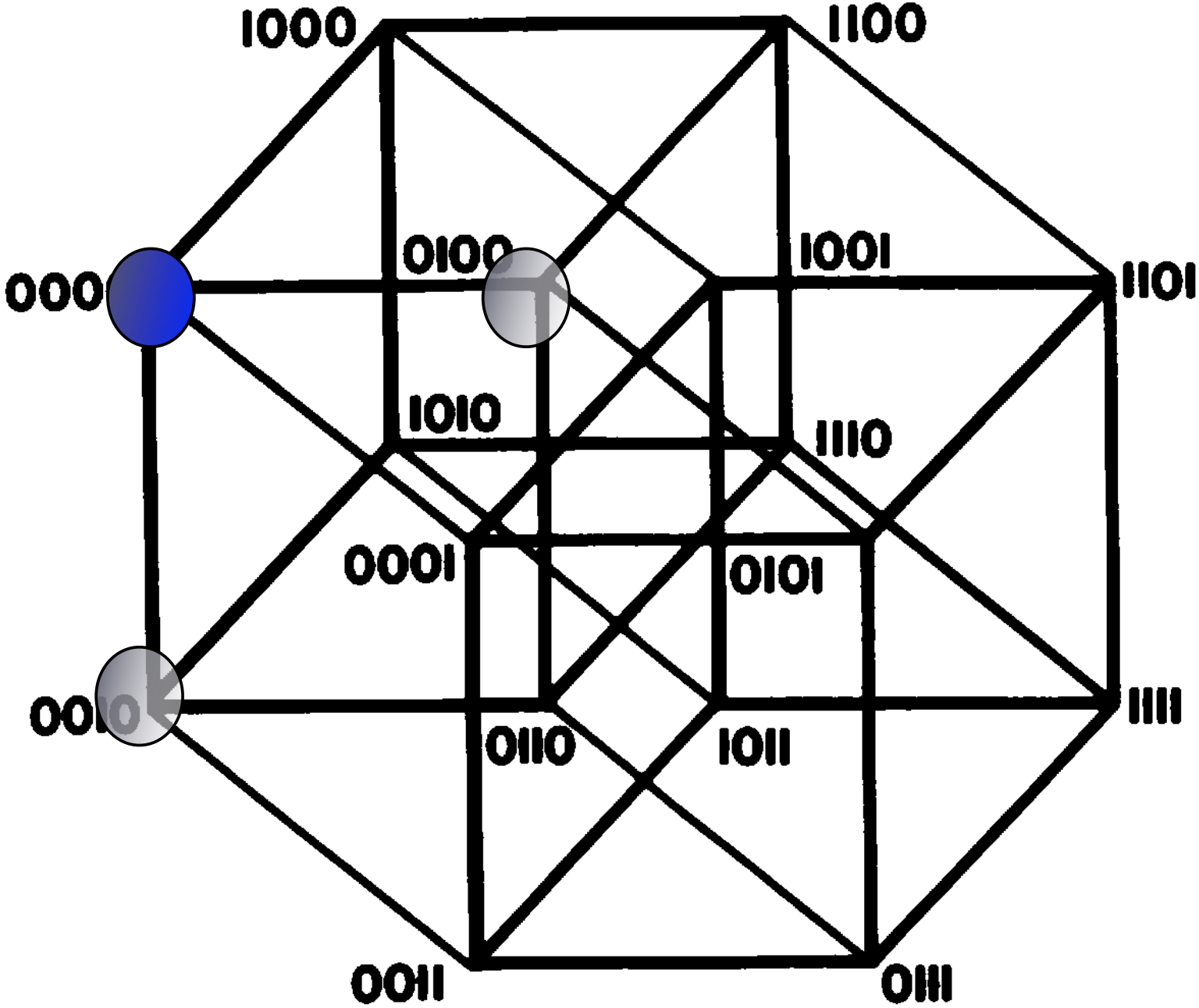
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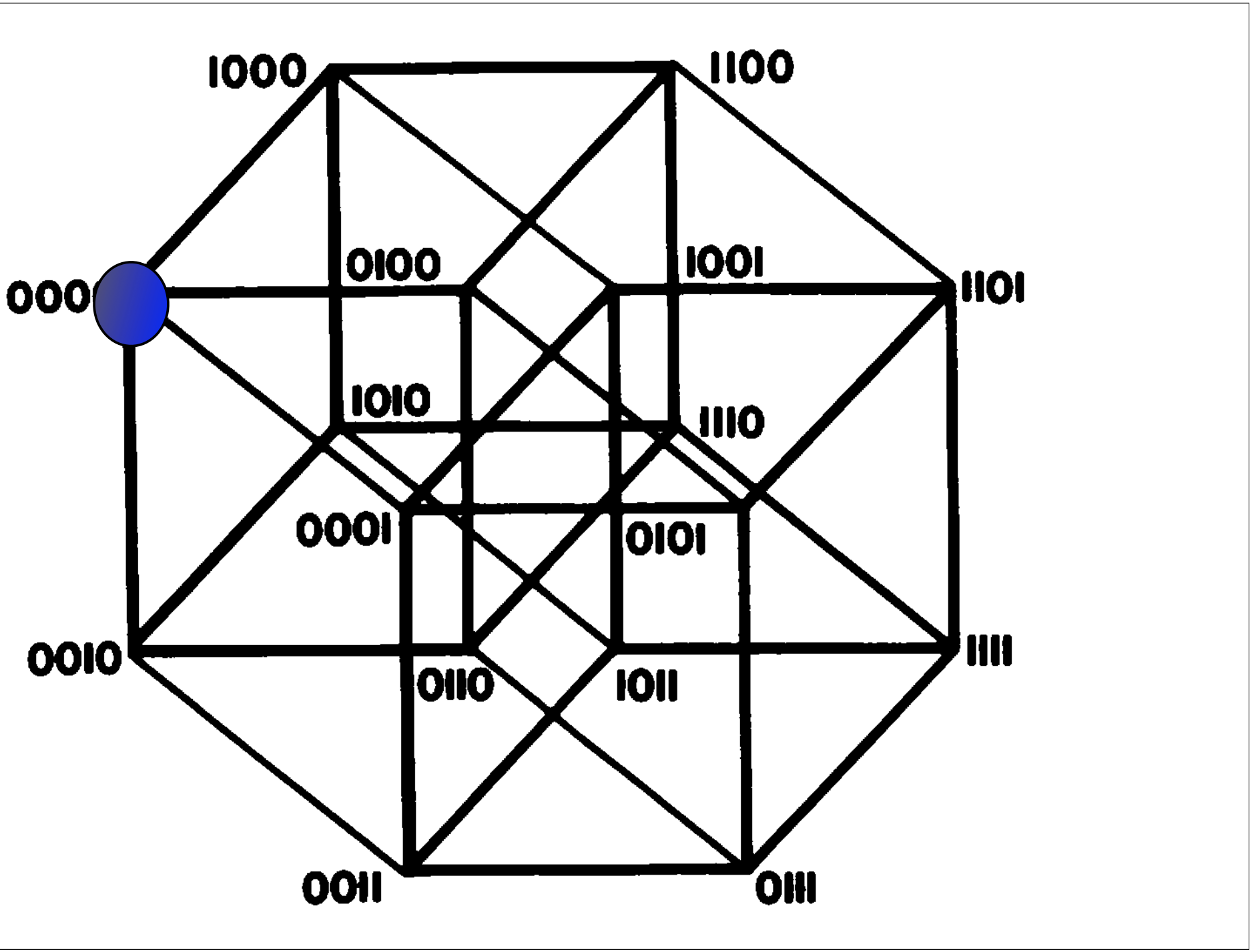
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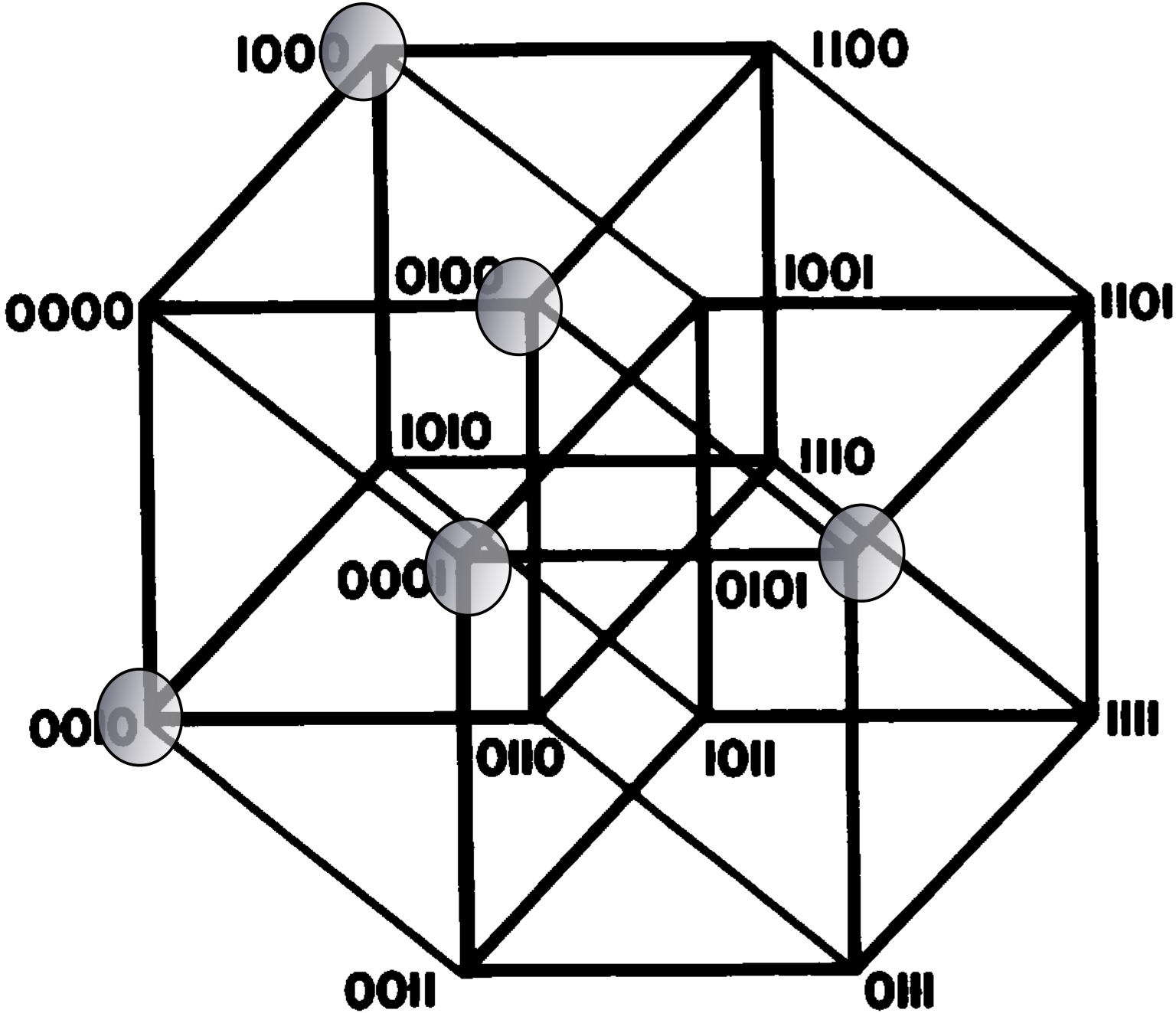
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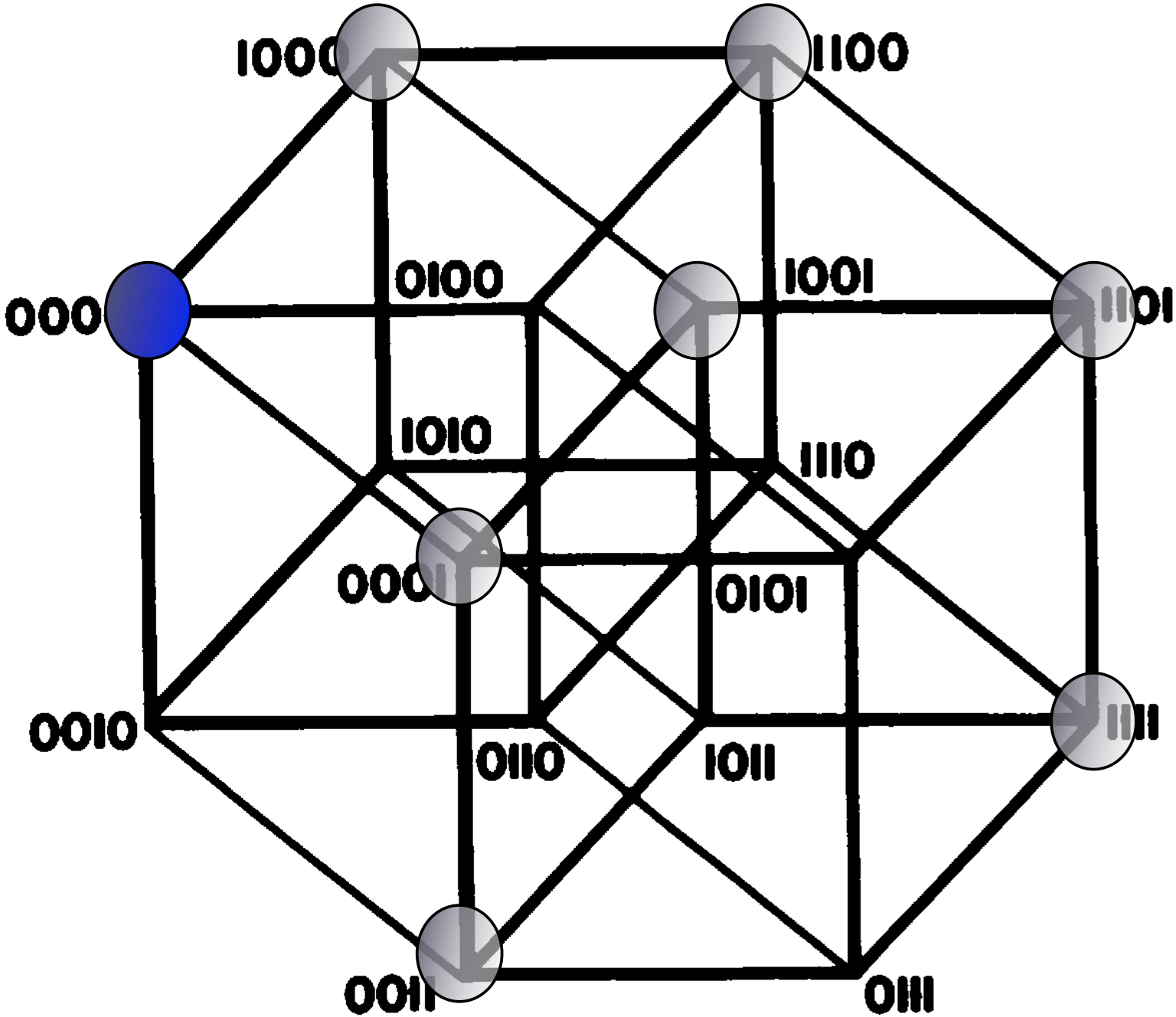
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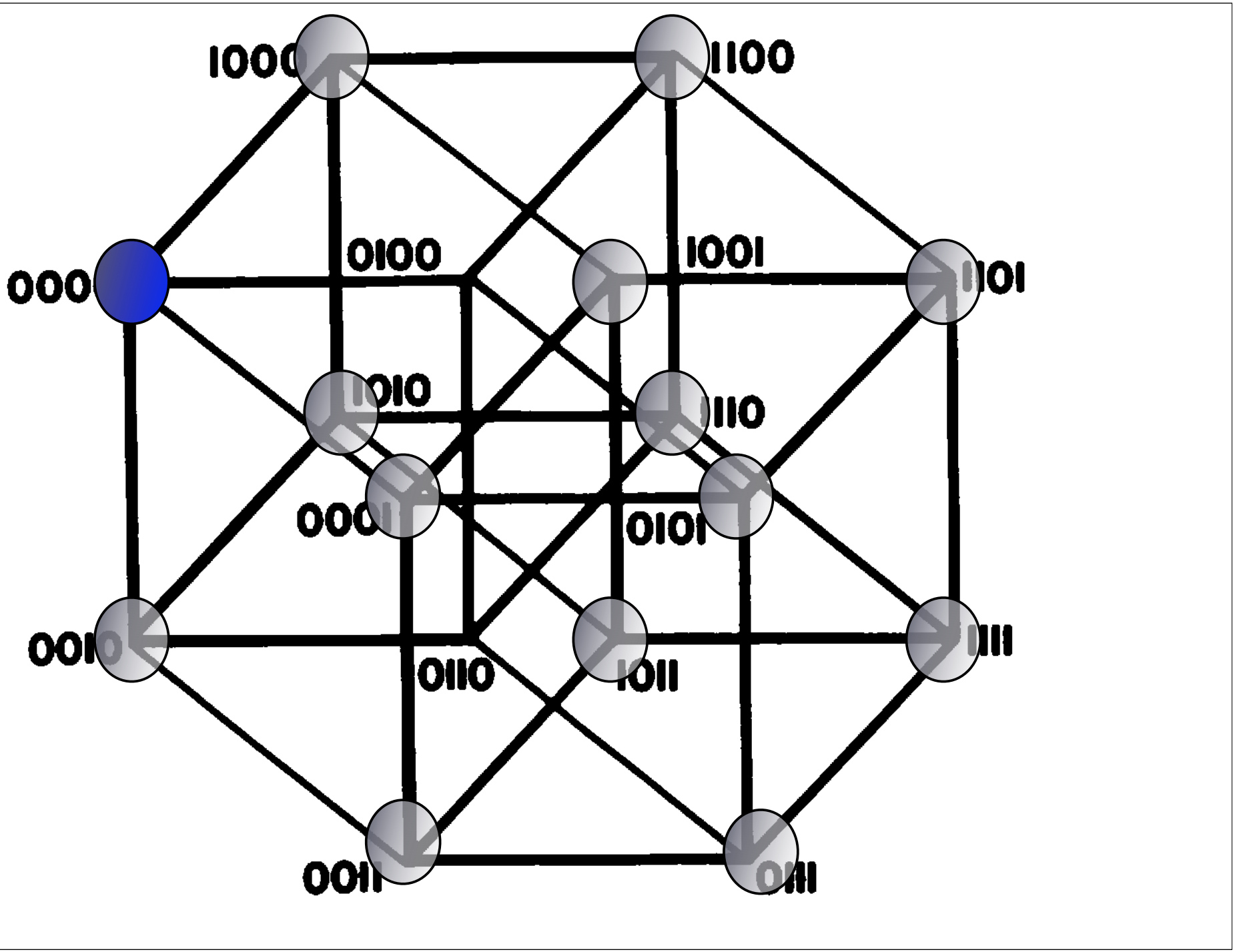
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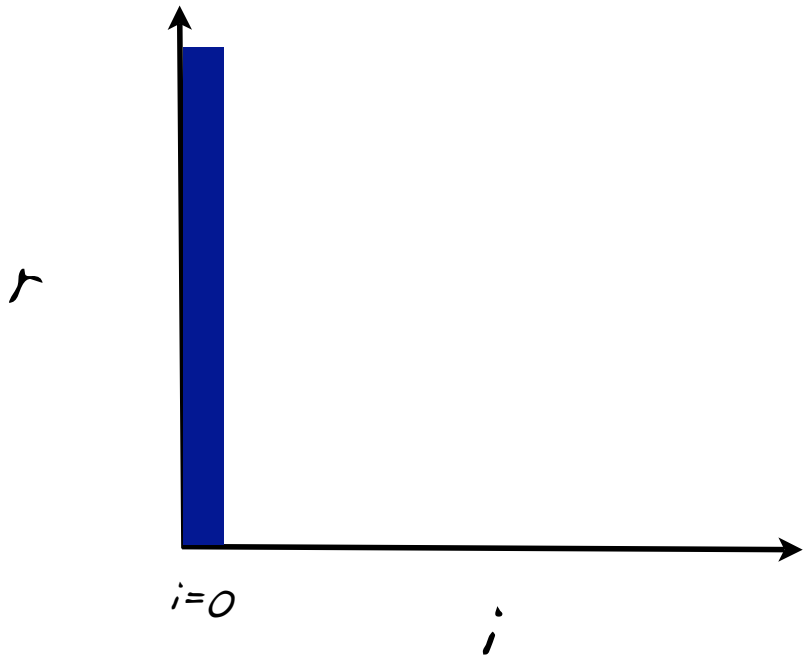
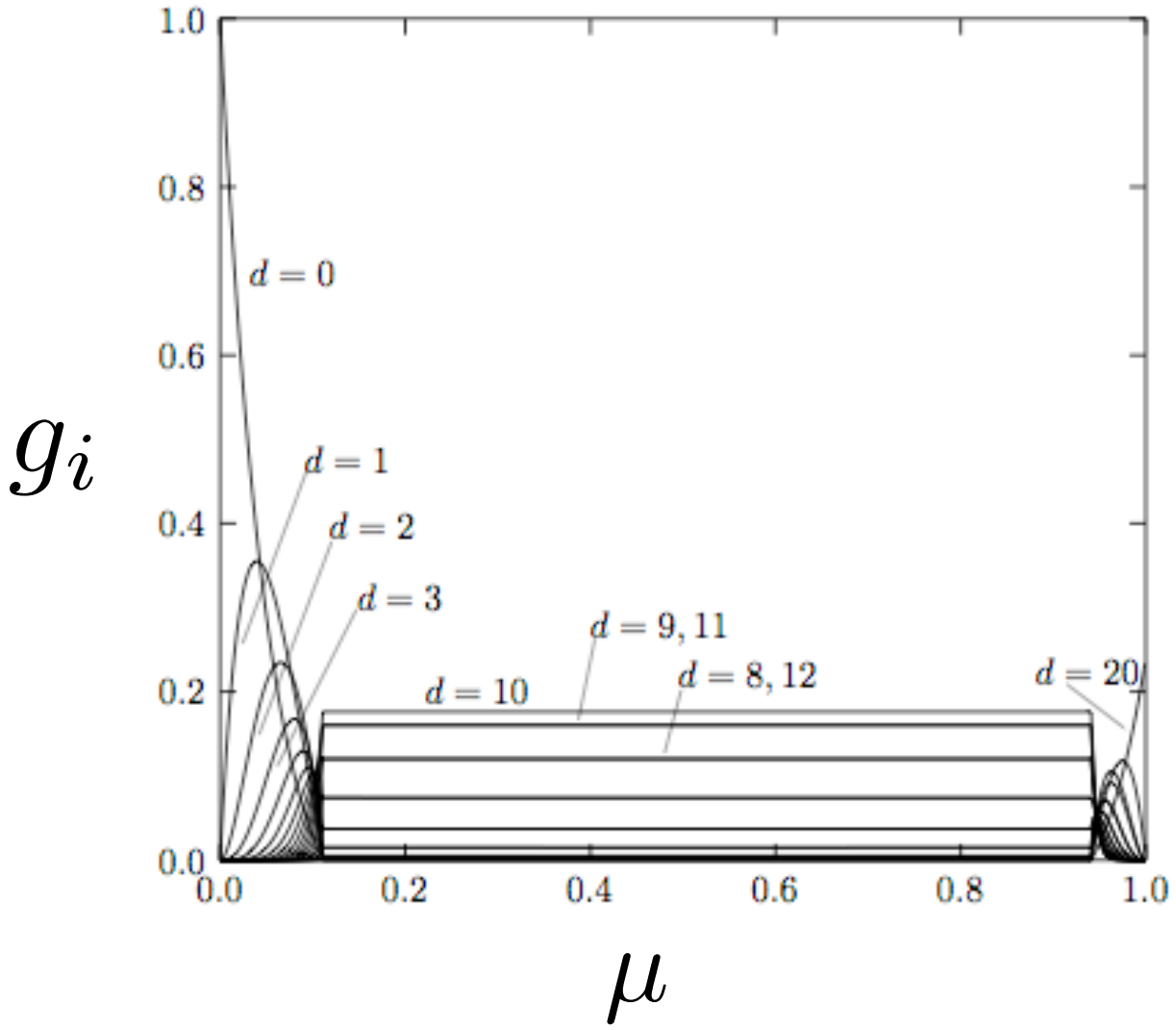
Delta-function landscape



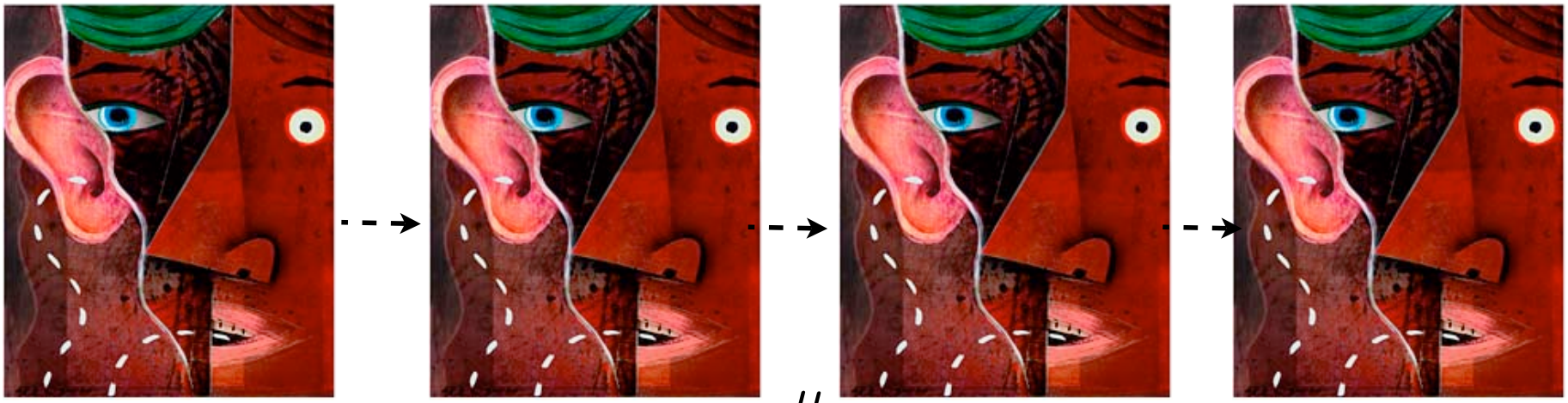
Error Threshold



Error Threshold

Delta function:

$$\mu < \frac{s}{L} = \frac{1}{L}$$



Fitness Landscape

Delta function:

$$\mu < \frac{s}{L} \approx \frac{1}{L}$$

Multiplicative function:

$$\mu < s$$

Introducing Phenotypes and hierarchical selection: deriving the *Price Equation*

$$\dot{E}[p] = Cov(r, p) + E[\dot{p}]$$

Insights from Page, Sigmund & others

$$\dot{g}_i = \sum_j^{2^n} g_j r_j(\mathbf{g}) m_{ji} - g_i \bar{f})$$

$$g_i \longrightarrow p_i$$

$$\bar{p} = E[p] = \sum_i p_i g_i$$

$$\dot{E}[p] = \sum_i p_i \dot{g}_i + \sum_i g_i \dot{p}_i$$

$$\dot{E}[p] = \sum_i p_i [\sum_j^{2^n} g_j r_j(\mathbf{g}) m_{ji} - g_i \bar{f})] + \sum_i g_i \dot{p}_i$$

$$\dot{E}[p] = \sum_{ij} p_i g_j r_j m_{ji} - \bar{r}\bar{p} + E[\dot{p}]$$

$$\dot{E}[p] = \sum_j p_j g_j r_j - \bar{r}\bar{p} + \sum_j g_j r_j \sum_i m_{ji}(p_i - p_j) + E[\dot{p}]$$

$$Cov(x, y) = E[(x - \mu)(y - \nu)] = E[xy] - \mu\nu$$

$$Cov(r, p) = \sum_j p_j g_j r_j - \bar{r}\bar{p}$$

$$E[r\Delta_m p] = \sum_j g_j r_j \sum_i m_{ji}(p_i - p_j)$$

$$\dot{E}[p] = Cov(r, p) + E[\dot{p}] + E[r\Delta_m p]$$

The Price Equation

Uses of Price Equation

- Fisher's fundamental theorem
- Kin selection (Hamilton's rule)
- Group selection
- Evolution of cooperation

Phenotypic Evolution

Deriving Adaptive Dynamics

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

$$\dot{E}[p] = Cov(r, p) + E[\dot{p}] + E[r\Delta_m p]$$

$$E[r\Delta_m p] = 0$$

$$E[\dot{p}] = 0$$

$$\dot{E}[p] = Cov(r, p) = Cov(r(p; g), p)$$

Taylor series

$$f(x) = \sum_{n=0}^{\infty} \frac{f^{(n)}(a)}{n!}(x-a)^n$$

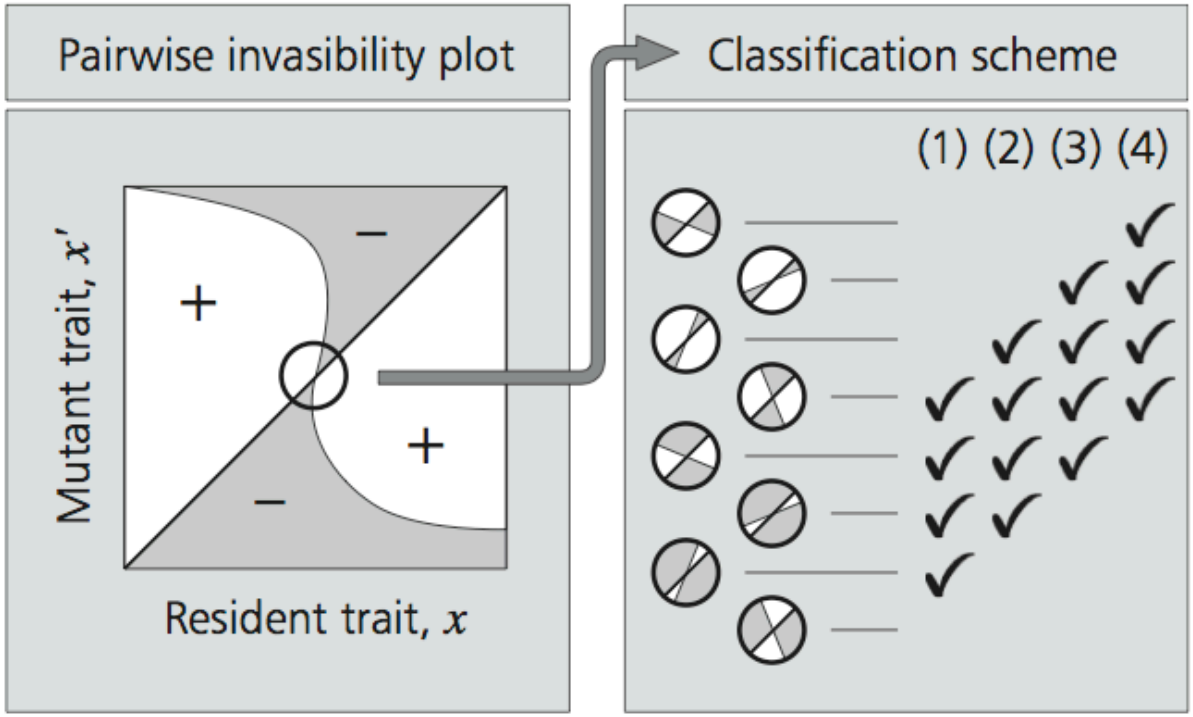
$$r(\bar{p}; g) = r(\bar{p}; g) + \frac{\delta r(a, x)}{\delta a}|_{a=p}(p - \bar{p})$$

$$\dot{E}[p] = Cov[p, r(\bar{p}; g) + \frac{\delta r(a, x)}{\delta a}|_{a=p}(p - \bar{p})]$$

$$\dot{E}[p] = Var(p)\frac{\delta r(a, x)}{\delta a}|_{a=p}$$

Adaptive Dynamics Equation

Evolutionary Game Theory: Adaptive Dynamics for Continuous Traits



$$\frac{dx}{dt} = \frac{1}{2}\mu\sigma^2\bar{N}(x)\frac{\delta f(x',x)}{\delta x'}\bigg|_{x'=x}$$

$$\dot{E}[p] = Var(p)\frac{\delta r(a,x)}{\delta a}|_{a=p}$$

Conclusions

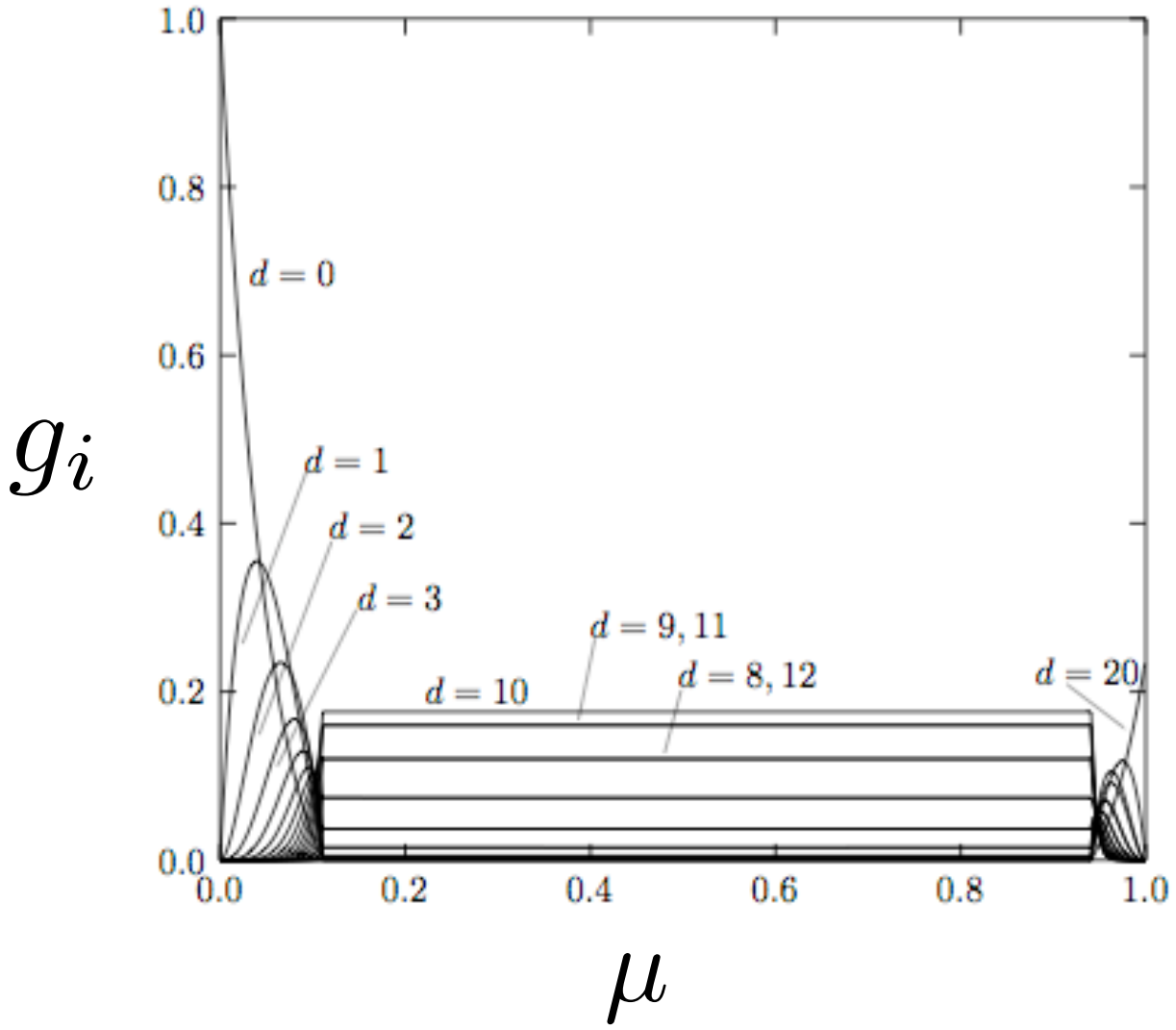
- Simple stoichiometry allows us to derive many of the fundamental equations of evolutionary dynamics
- These equations tell us how total genomic information is constrained by mutation rates
- Allow us to study game dynamics in an evolutionary and ecological framework
- Through AD Provide the basis for most current studies on cooperation, kin & group selection, microbial dynamics and cultural/language evolution.

Not all the gold that is beneath the moon,
Or ever hath been, of these toil-worn souls
Might purchase rest for one.

Canto VII., lines 65—67.

Implications (with a few extra assumptions)

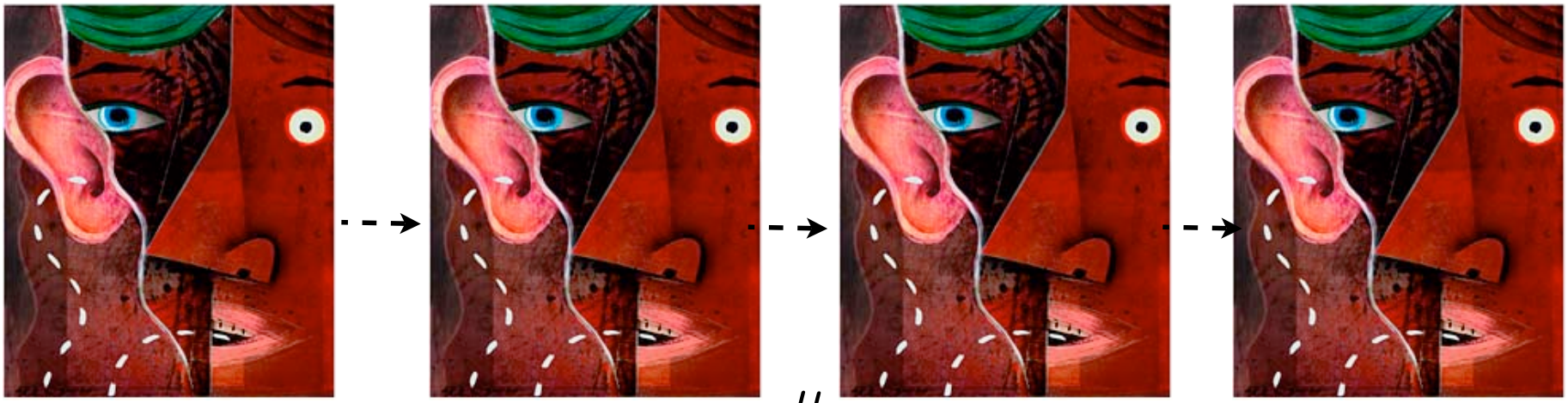
Error Threshold



Error Threshold

Delta function:

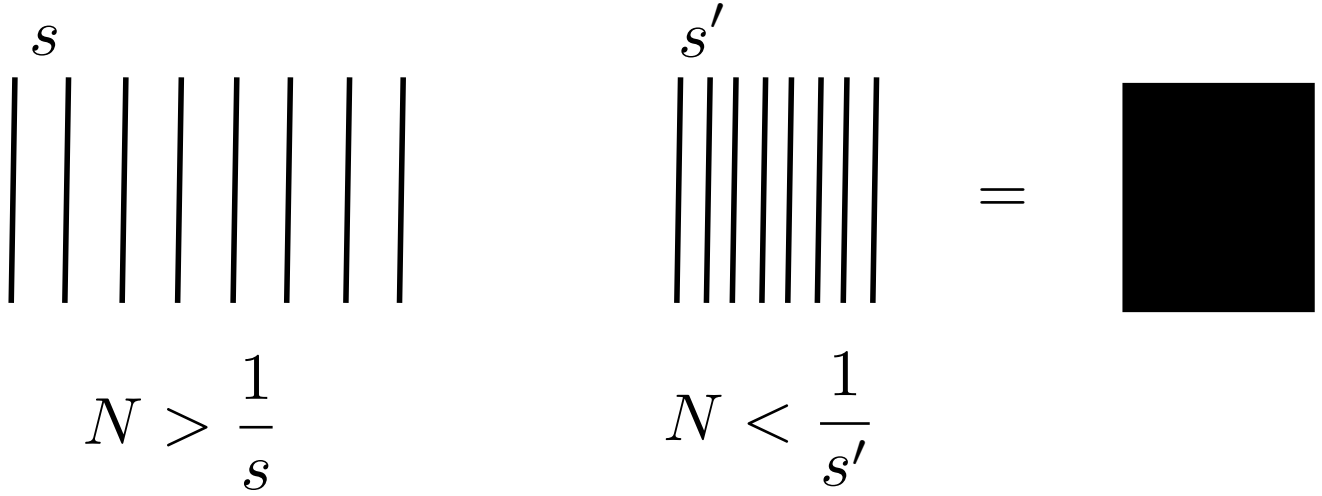
$$\mu < \frac{s}{L} = \frac{1}{L}$$



Kimura's Neutrality Inequality

Condition for Neutrality

$$sN < 1$$



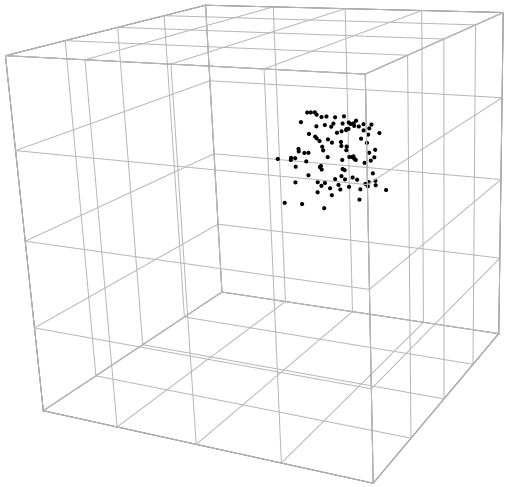
Evolution's Arrow

Eigen-Kimura Information Storage Principle

Evolutionary Information Storage

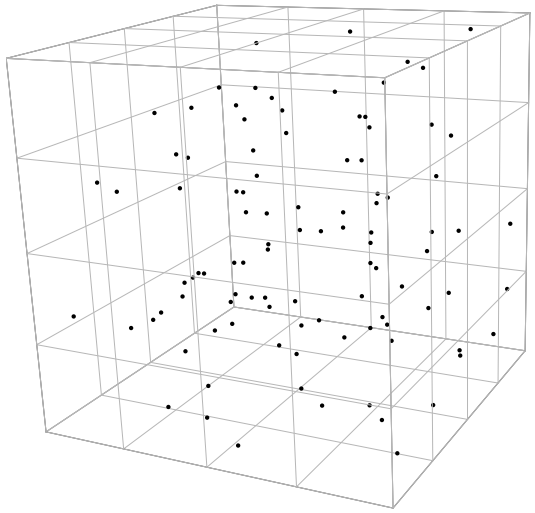
Information Conserved

$$\mu L < 1 < sN$$



Information Lost

$$\mu L > 1 < sN$$
$$\mu L < 1 > sN$$
$$\mu L > 1 > sN$$

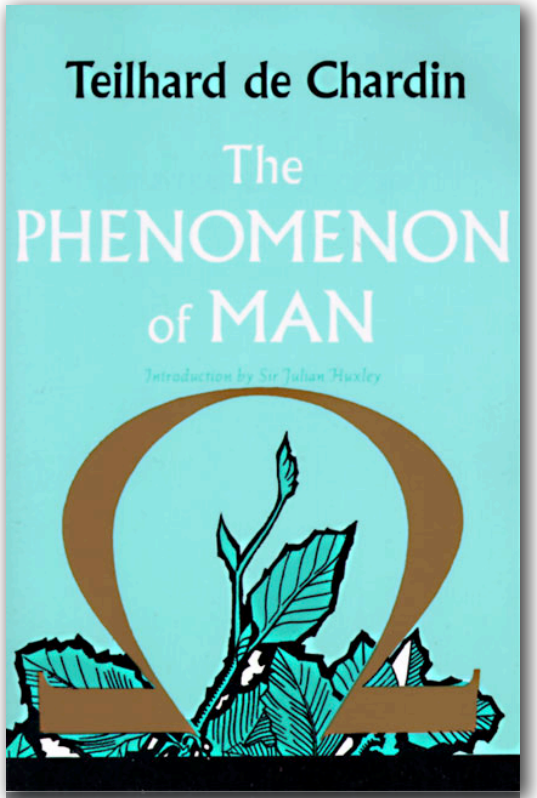


"Darwinian" Selection for Compression

$$\mu L < 1 < sN$$

$$sN > \mu L$$

The Preference for Population Multiplicity & Individual Minimality & Fidelity


Teilhard de Chardin
The
PHENOMENON
of MAN
Introduction by Sir Julian Huxley

So What's Missing?

Frontiers

Select Bibliography

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- Sigmund K. Hofbauer, J, Evolutionary Games and Population Dynamics. 1998
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