

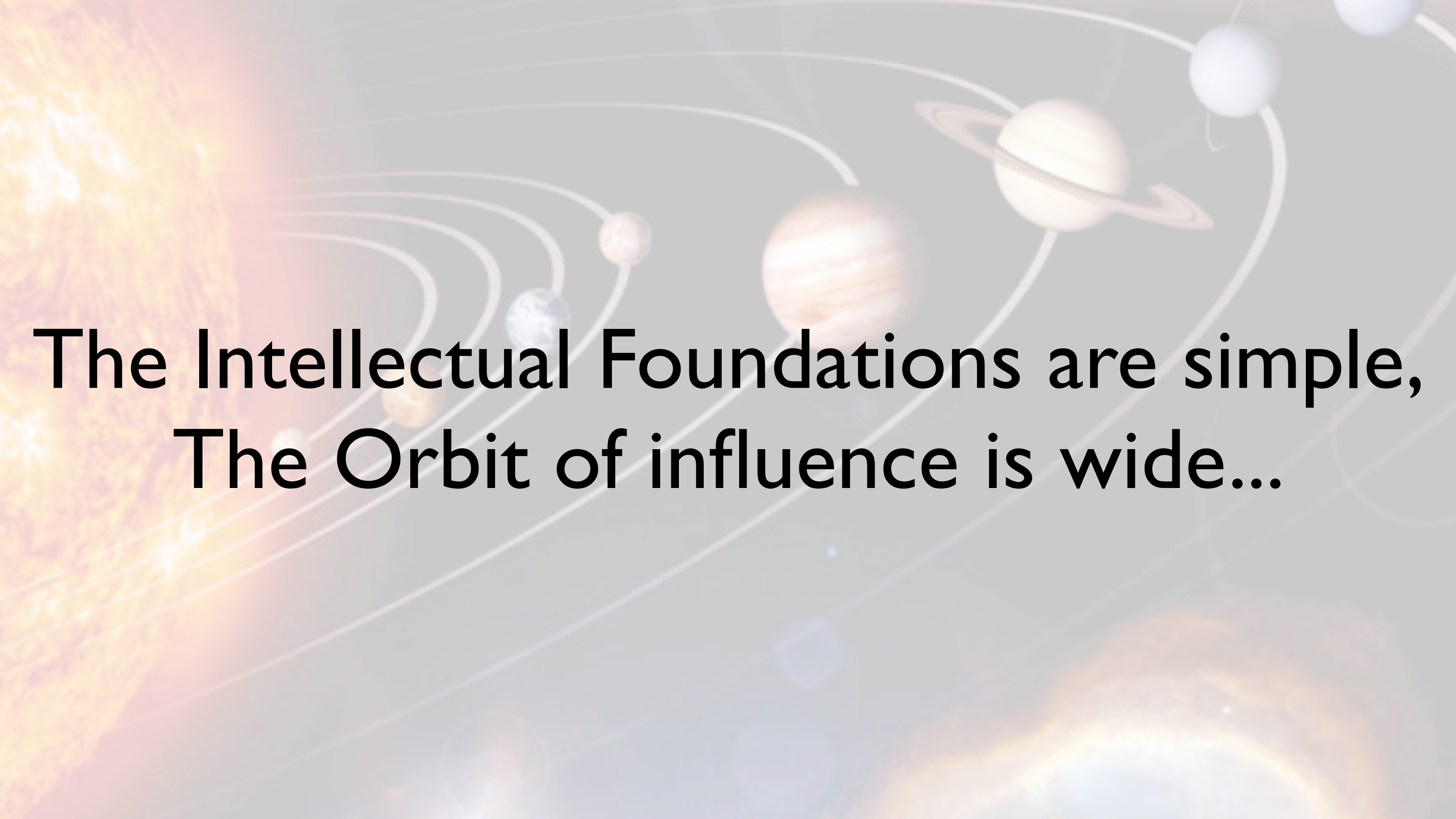
Evolutionary Dynamics

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Evolutionary Theory - specialities

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

Ceci n'est pas une pipe.



**The Intellectual Foundations are simple,
The Orbit of influence is wide...**

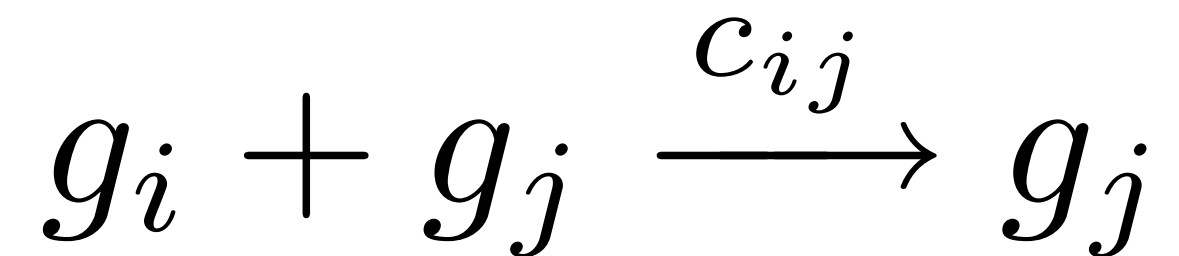
Evolutionary Stoichiometry

replication

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

Evolutionary Stoichiometry

competition



Evolutionary Stoichiometry

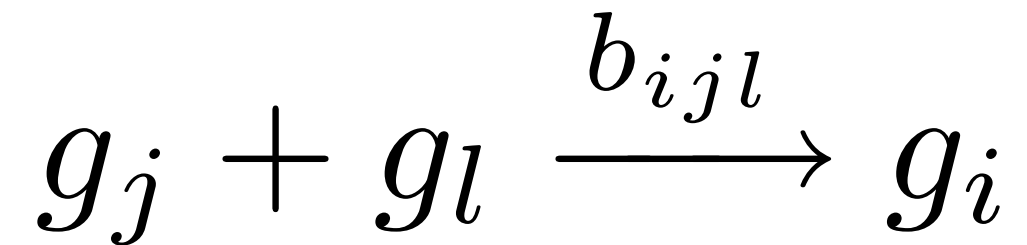
mutation

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

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

Evolutionary Stoichiometry

recombination



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

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

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

Evolutionary Stoichiometry

Development

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

Typically Treated Thus

$g_i \xrightarrow{d_i} p_i$

Replicator Equation

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

$$g_i + g_j \xrightarrow[r_j]{c_{ij}} g_j$$

n genomes

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

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

$$\sum g_i(t=0) = 1$$

Evolutionary Game Theory: Frequency dependent Replicator Equation

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

$$g_i + g_j \xrightarrow[r_j]{c_{ij}} g_j$$

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

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

Payoff Matrix $P = [p_{ij}]$

with linear payoffs:

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

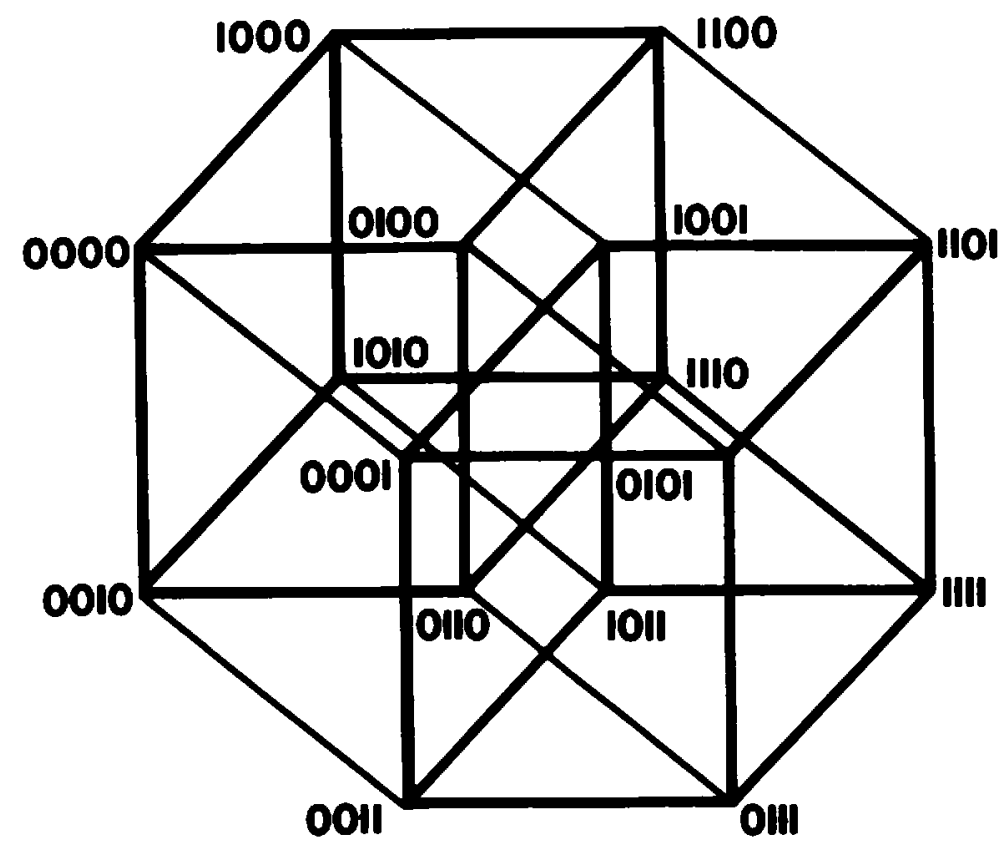
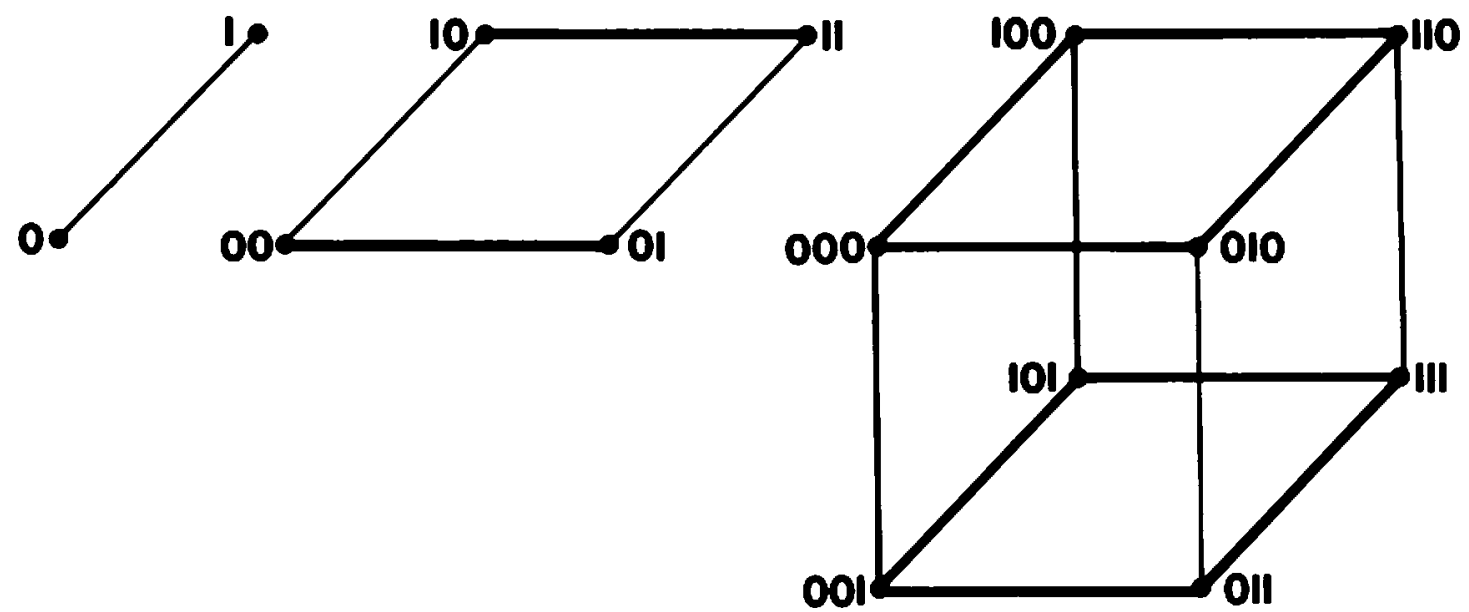
Evolutionary Game Theory: Frequency dependent Replicator Equation

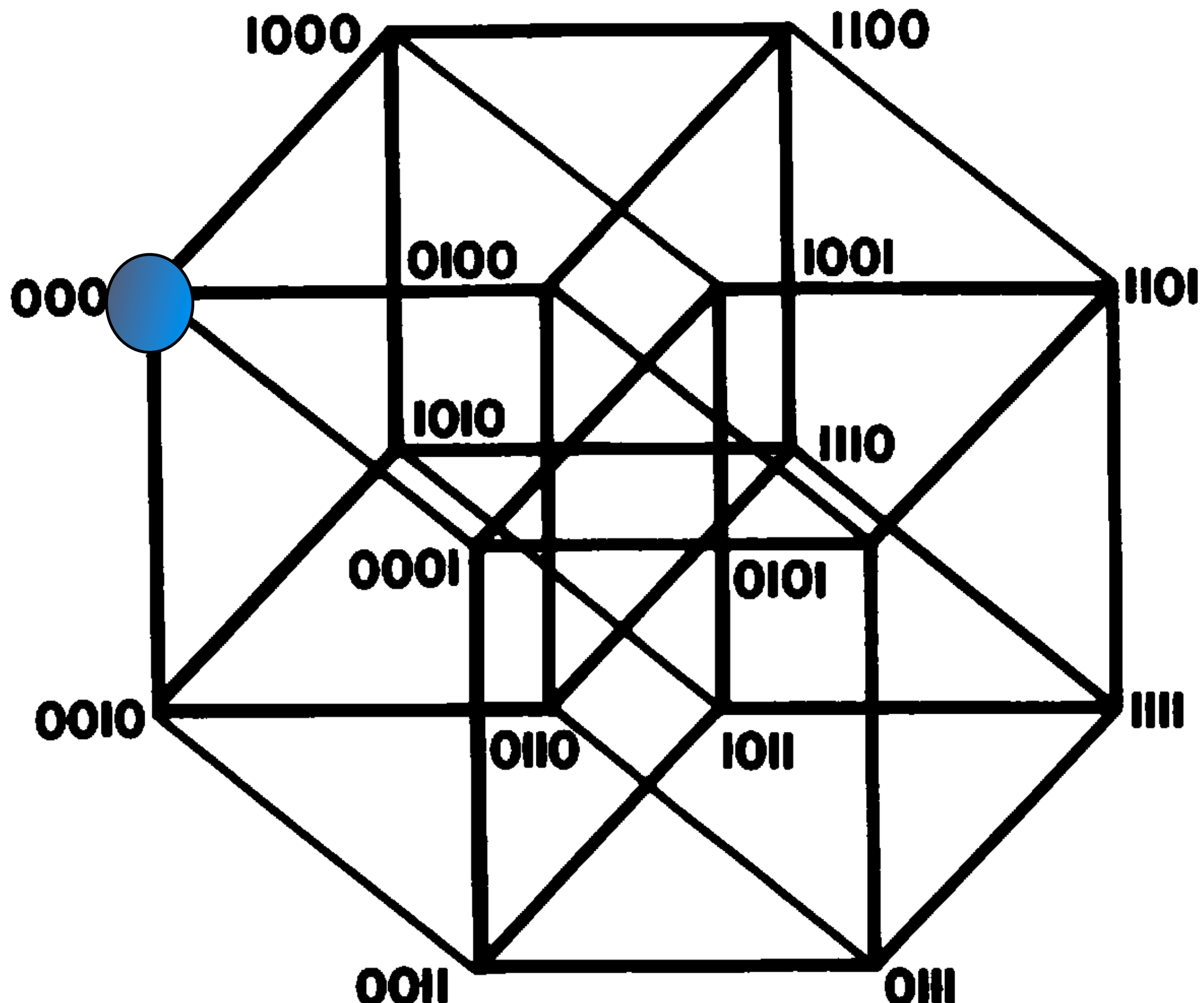
$$\dot{g}_i = g_i \left(\sum_j^n g_j p_{ij} - \sum_j^n g_j \sum_k^n g_k p_{jk} \right)$$

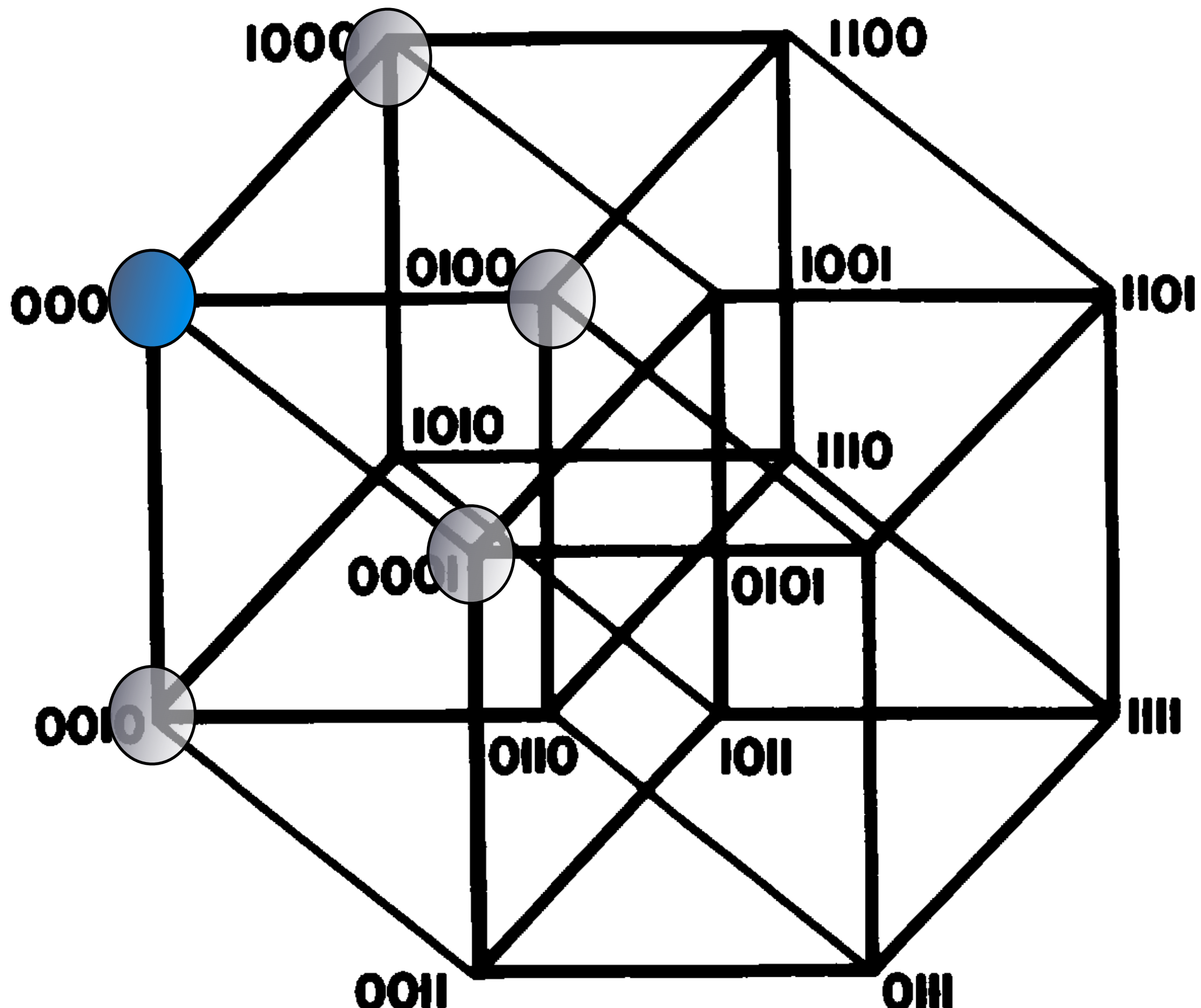
Stable Equilibria of Replicator Eq. and Nash Equilibria

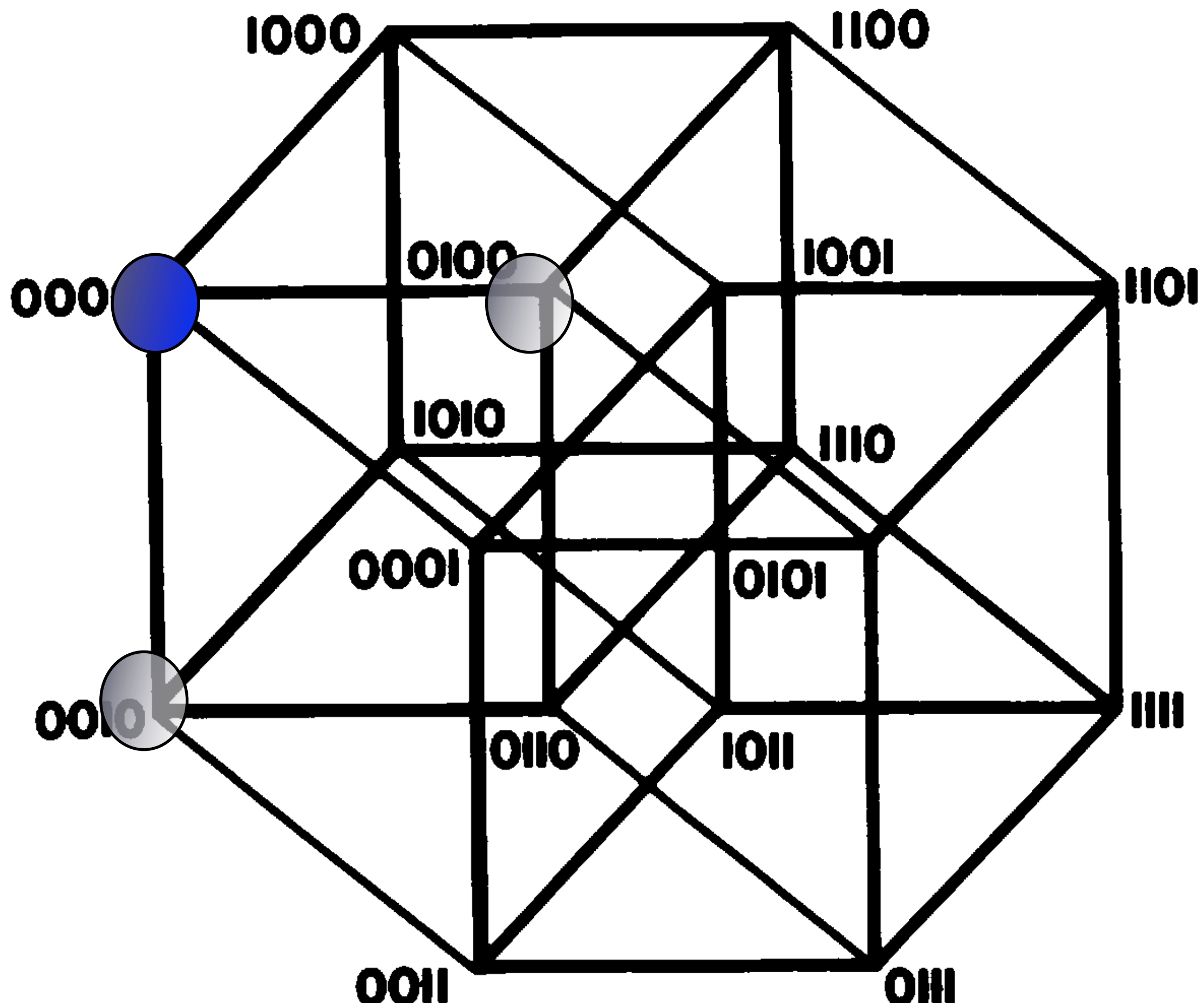
Mathematica Demo

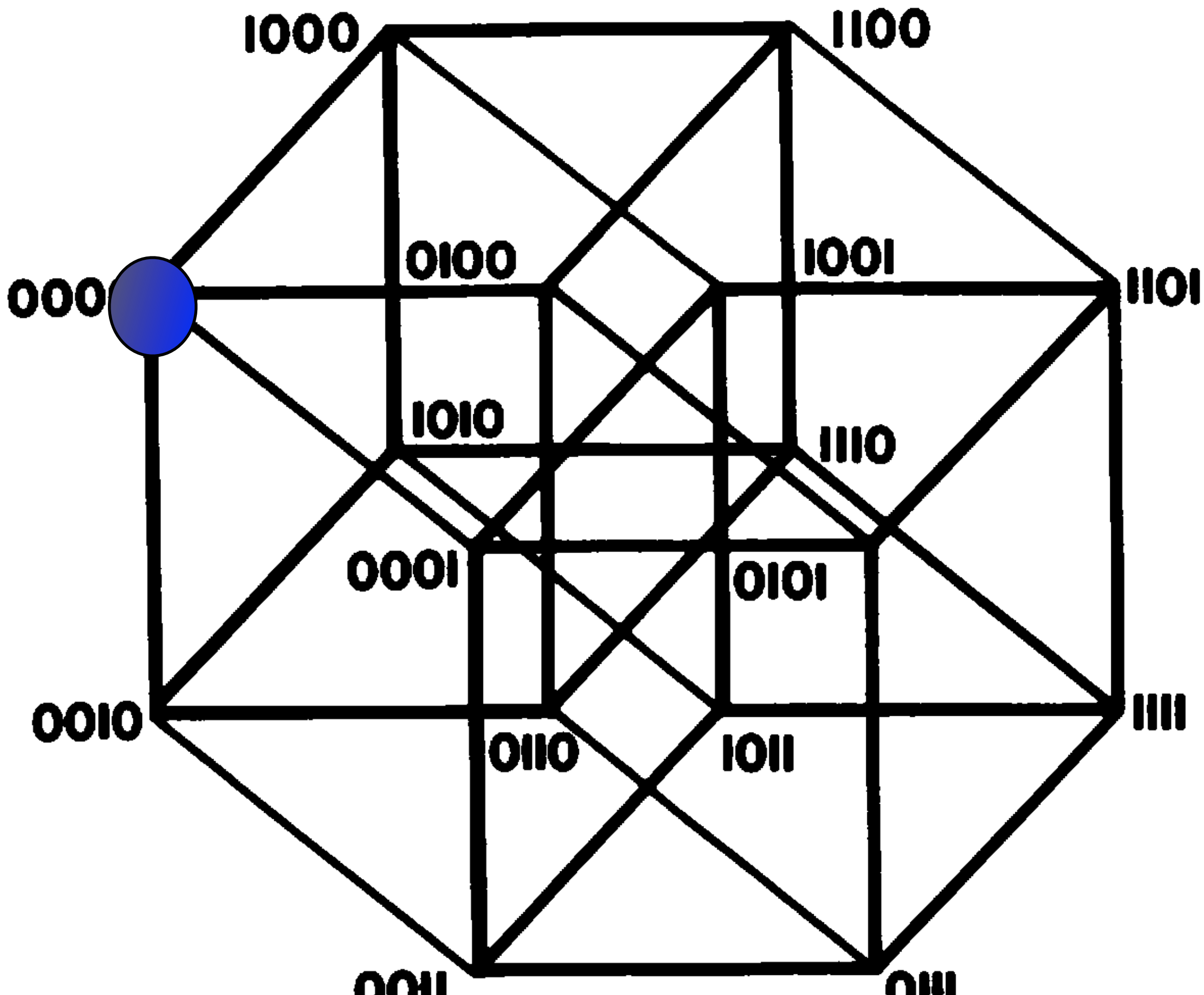
Mutation & Sequence Space

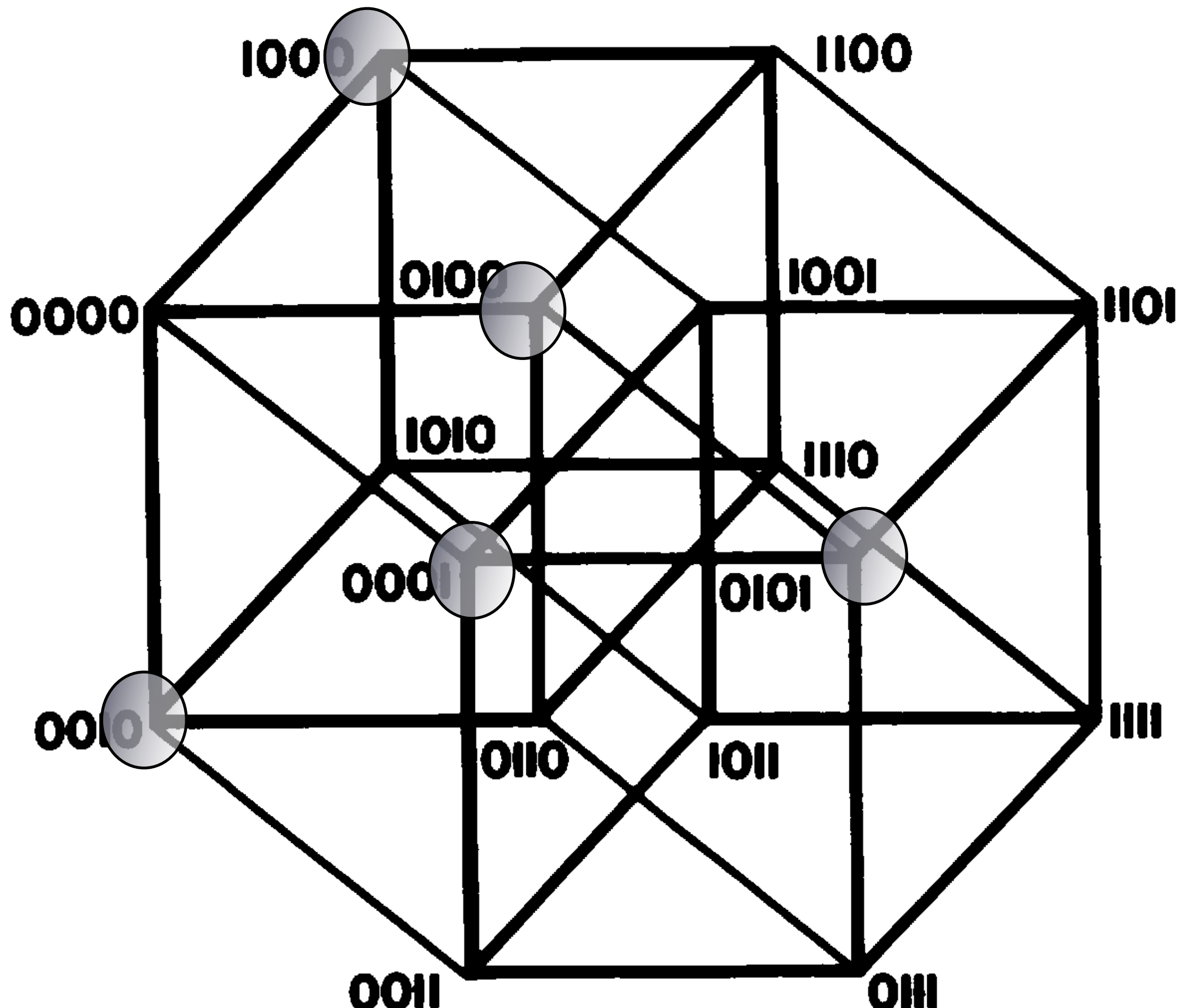


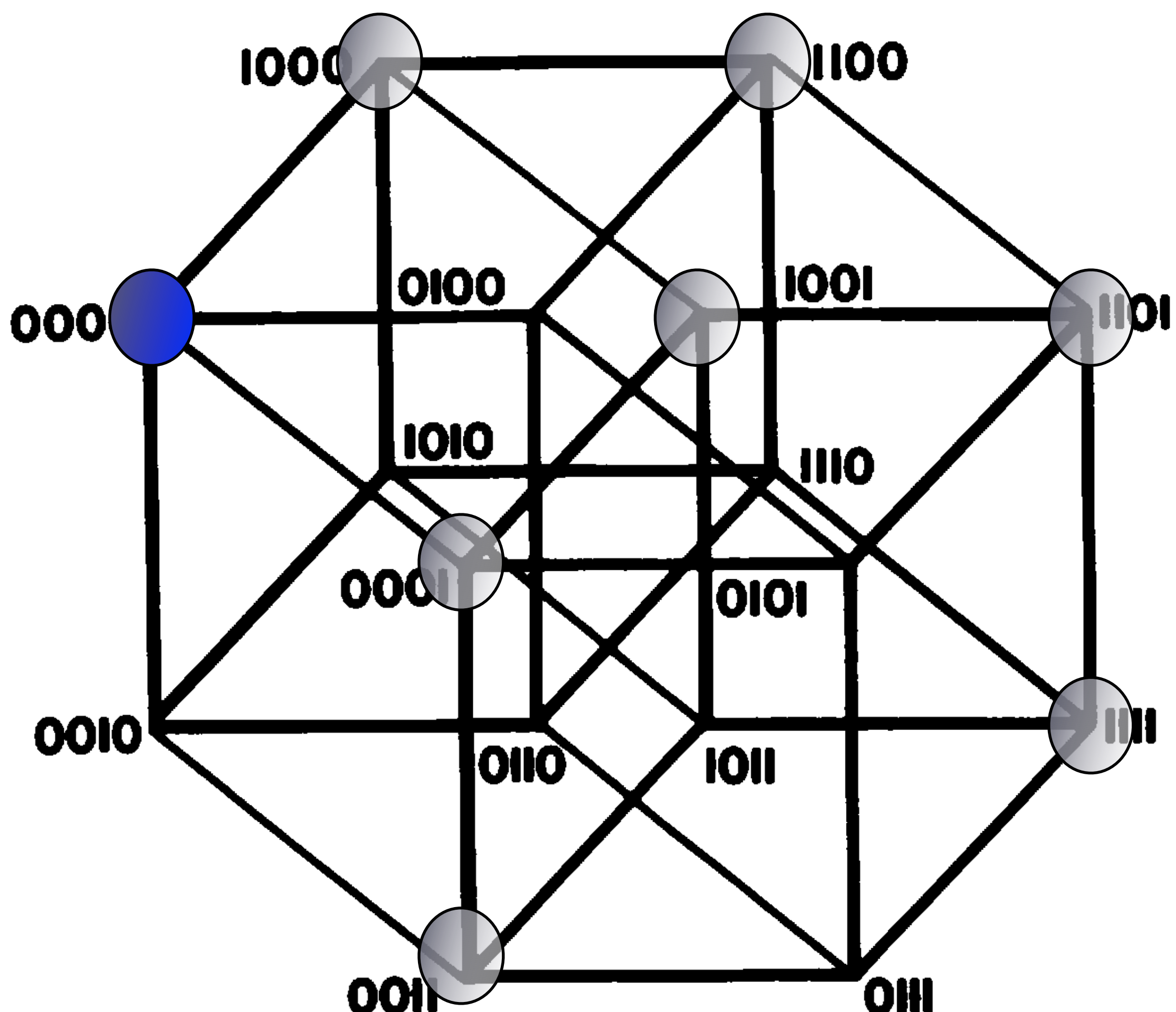


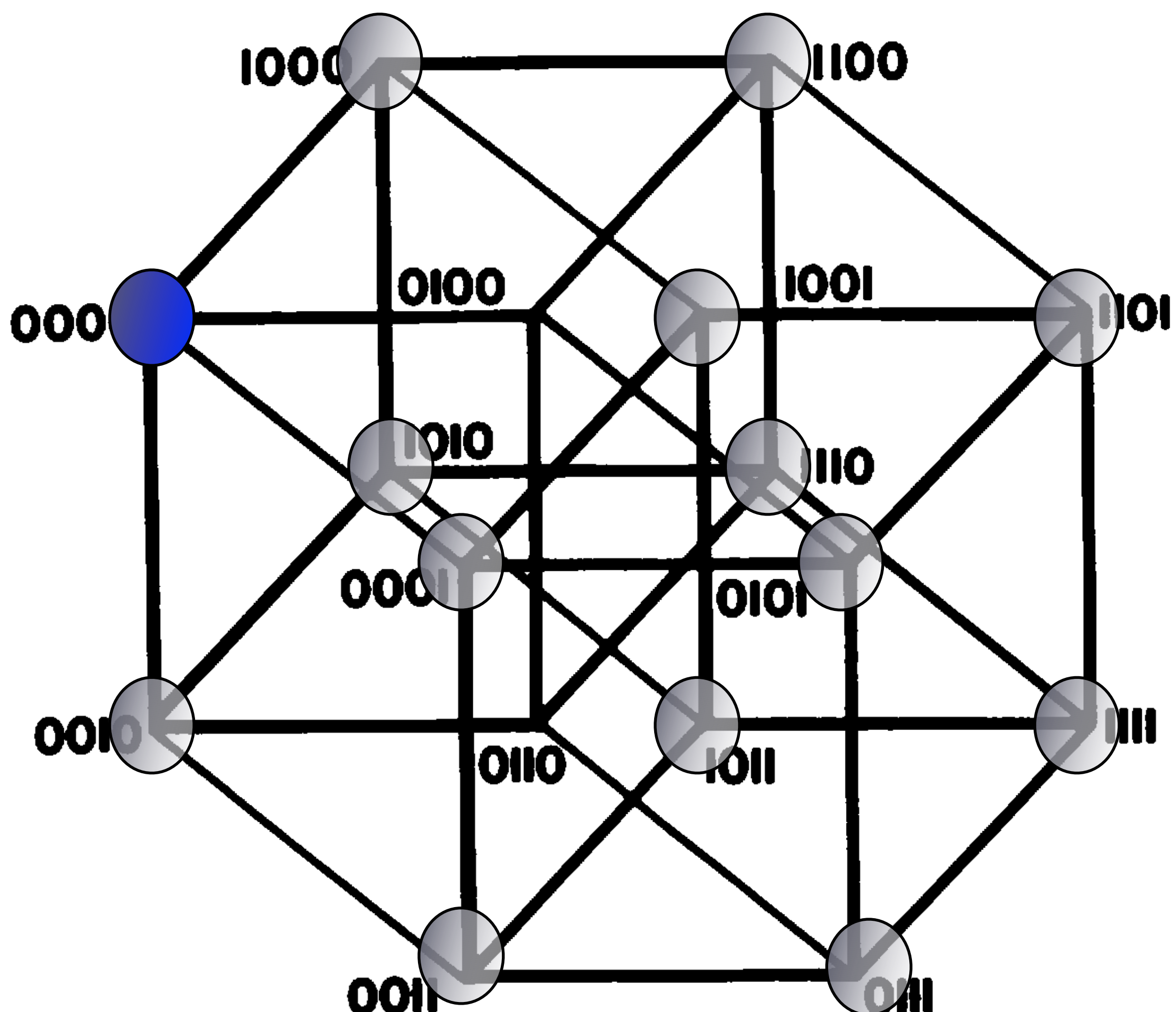












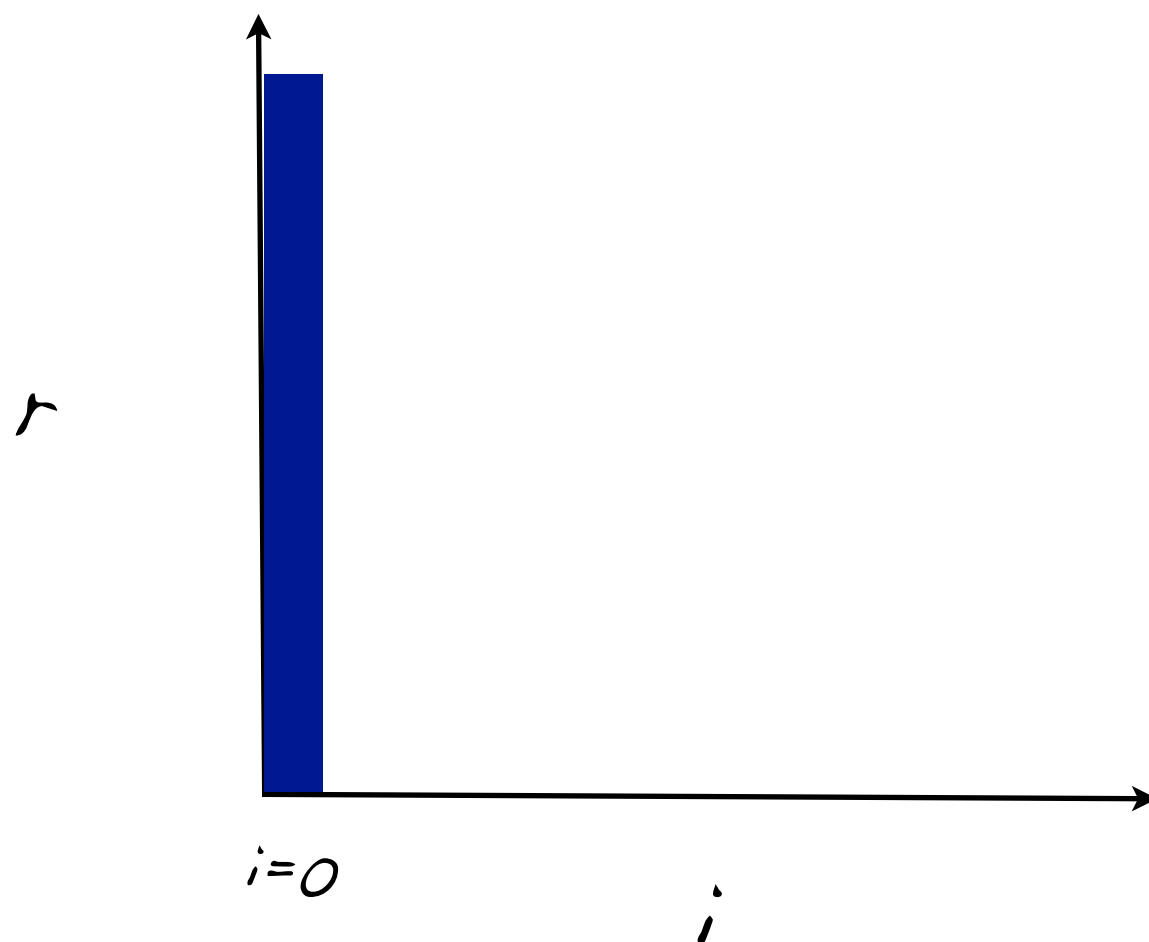
Replicator-Mutator Equation

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

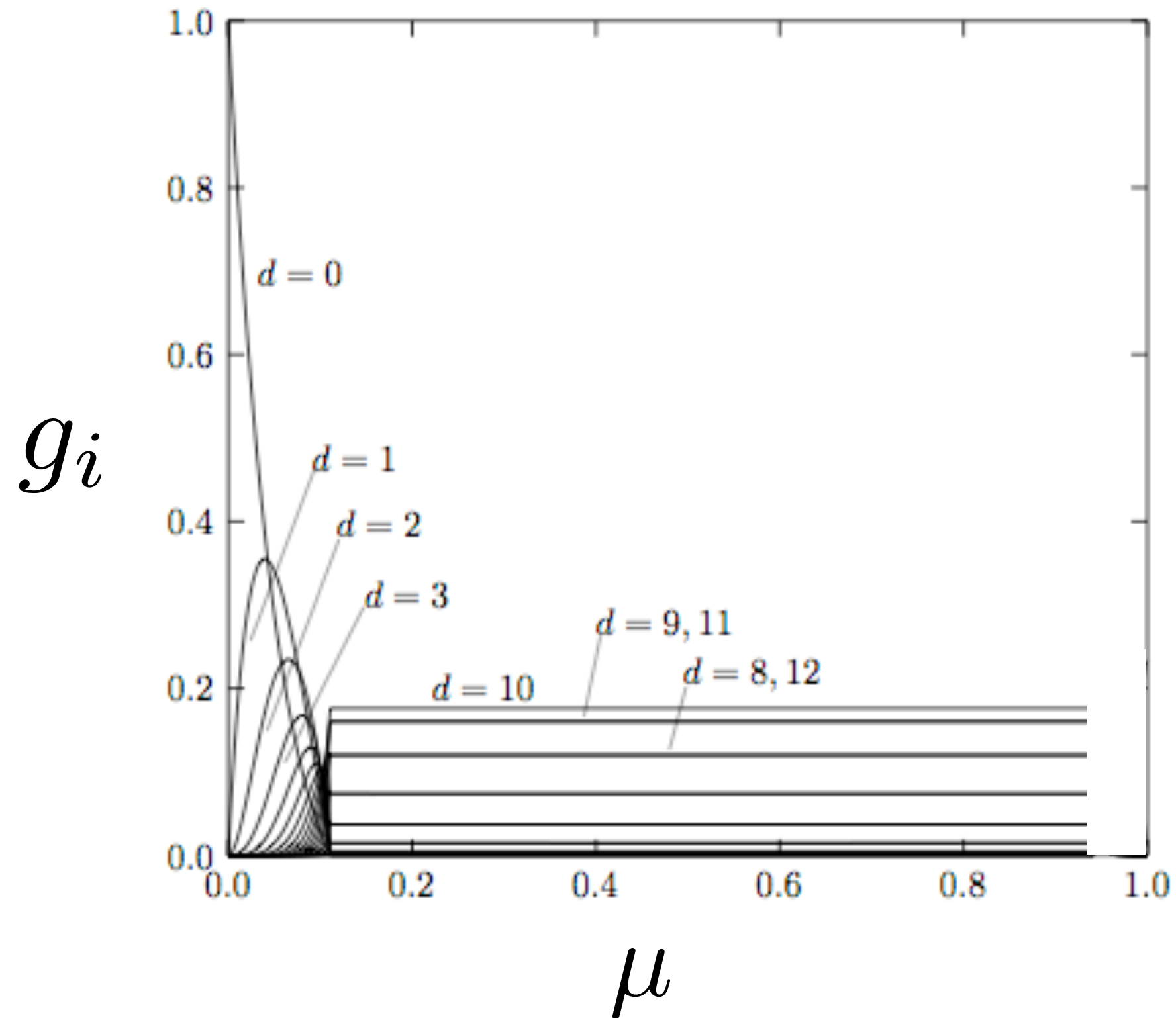
$$m_{ij} = \mu^{H(i,j)} (1 - \mu)^{L-H(i,j)}$$

Curious Implications....

Delta-function landscape



Error Threshold



Error Threshold

Delta function:

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



$L = 1$



μ



$L = 2$



μ



$L = 3$



μ



$L = 4$

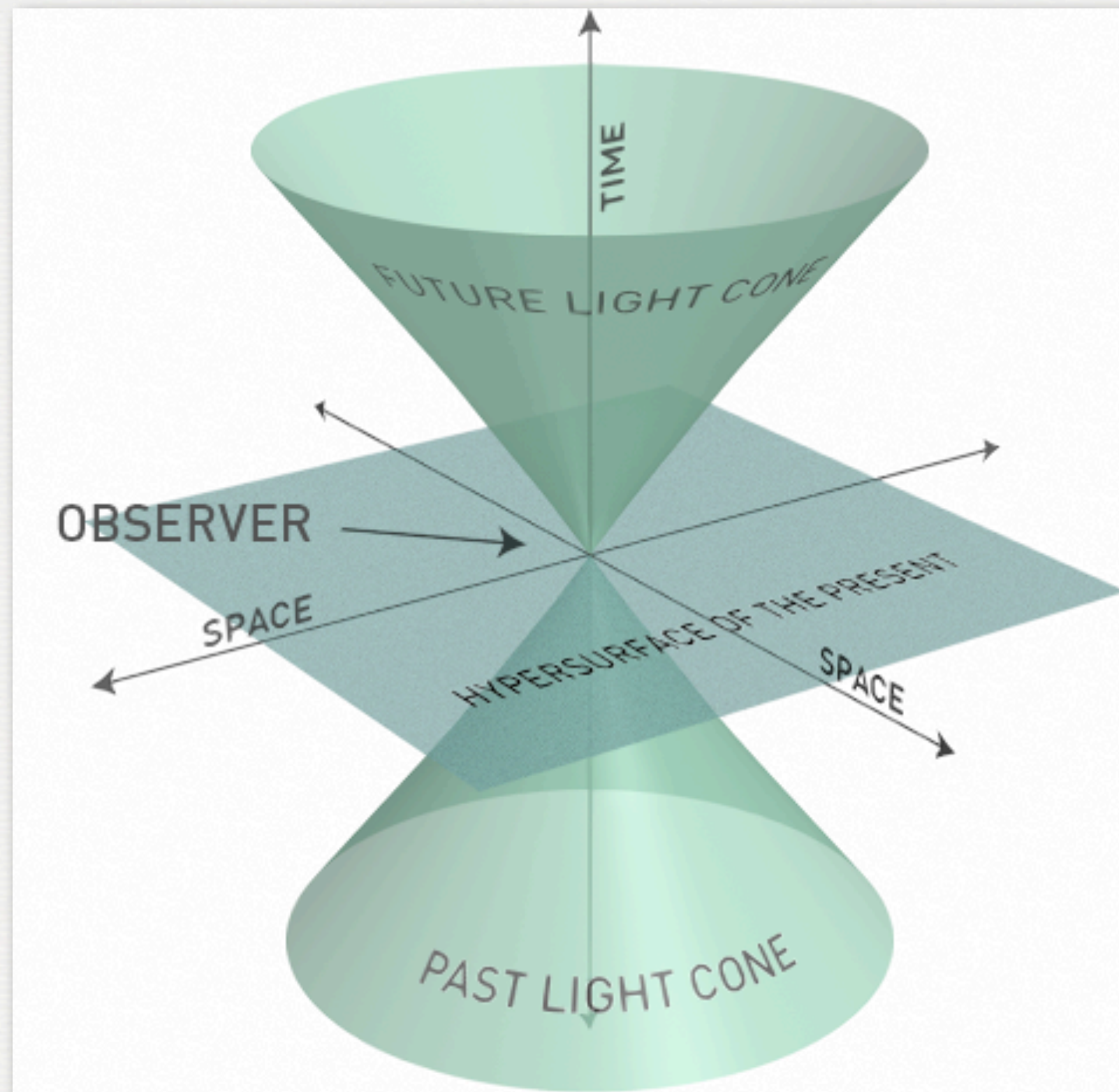
Fitness Landscape

Delta function:

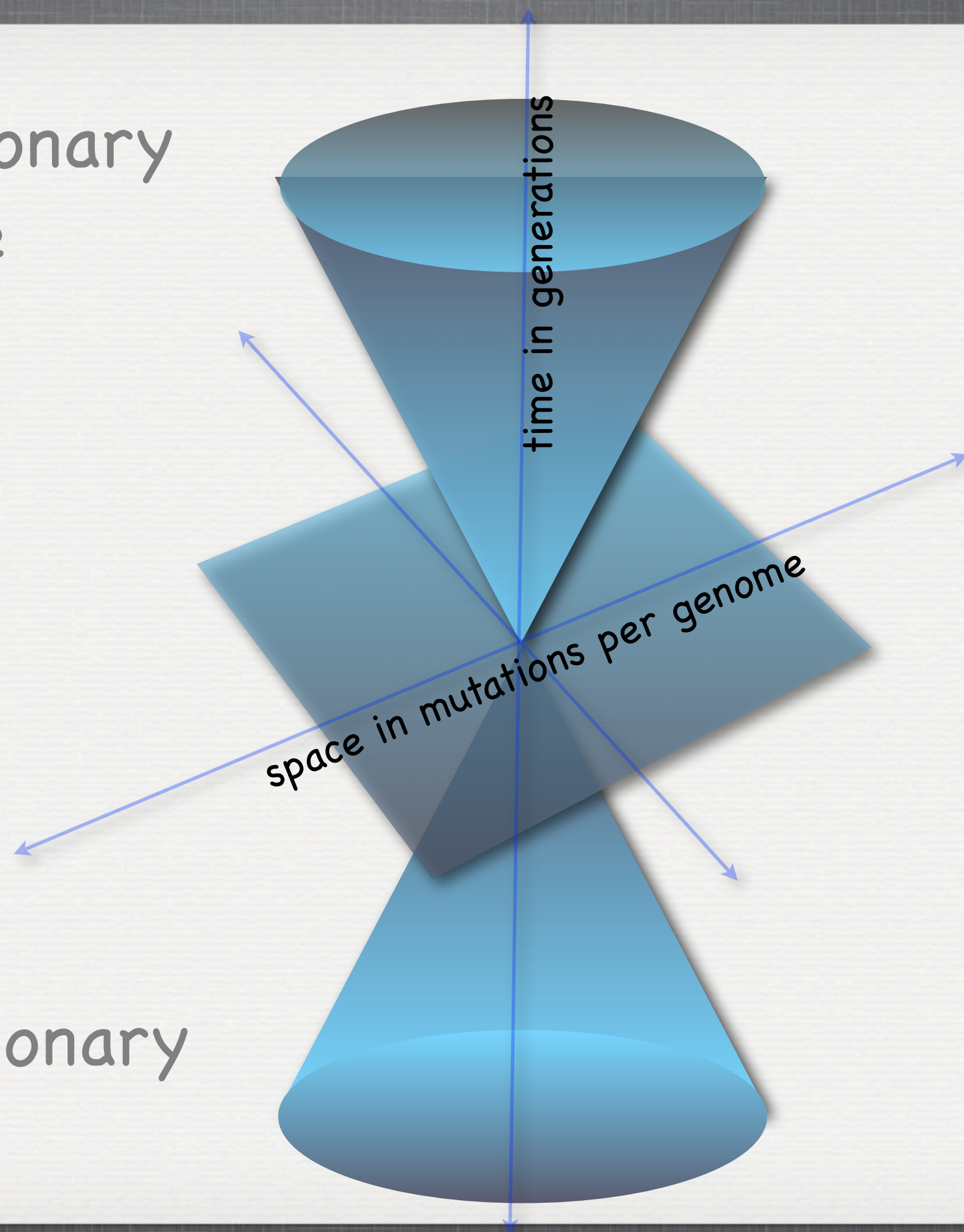
$$\mu < \frac{s}{L} \approx \frac{1}{L}$$

Multiplicative function:

$$\mu < s$$



The evolutionary
future

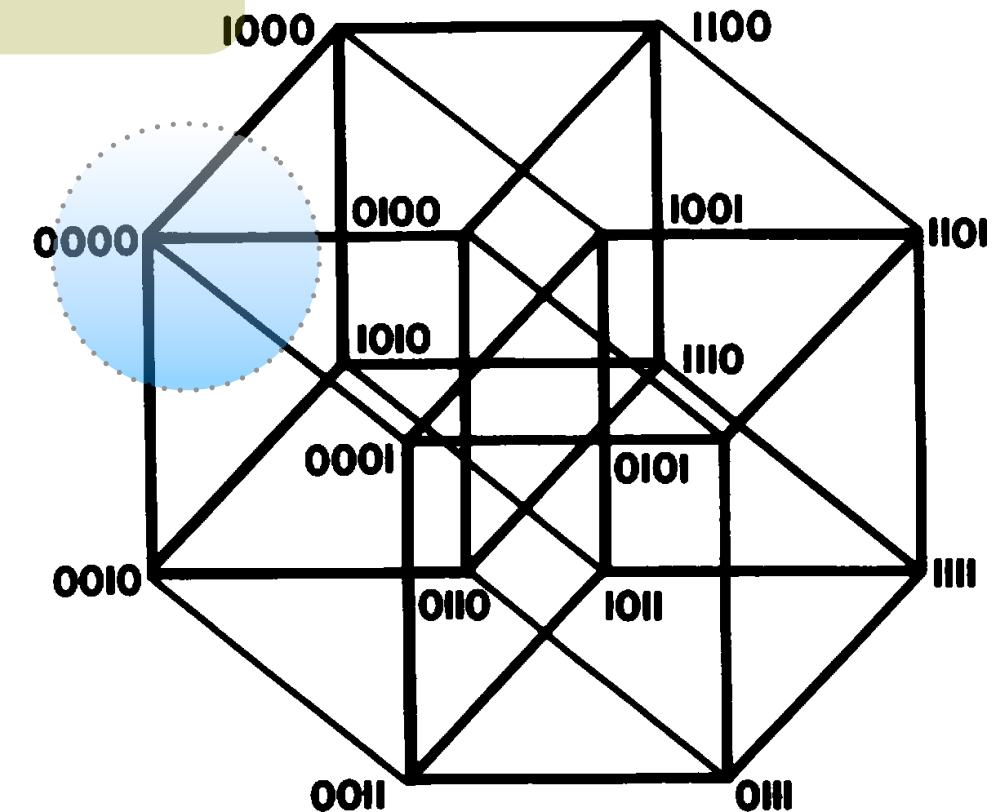


The evolutionary
past

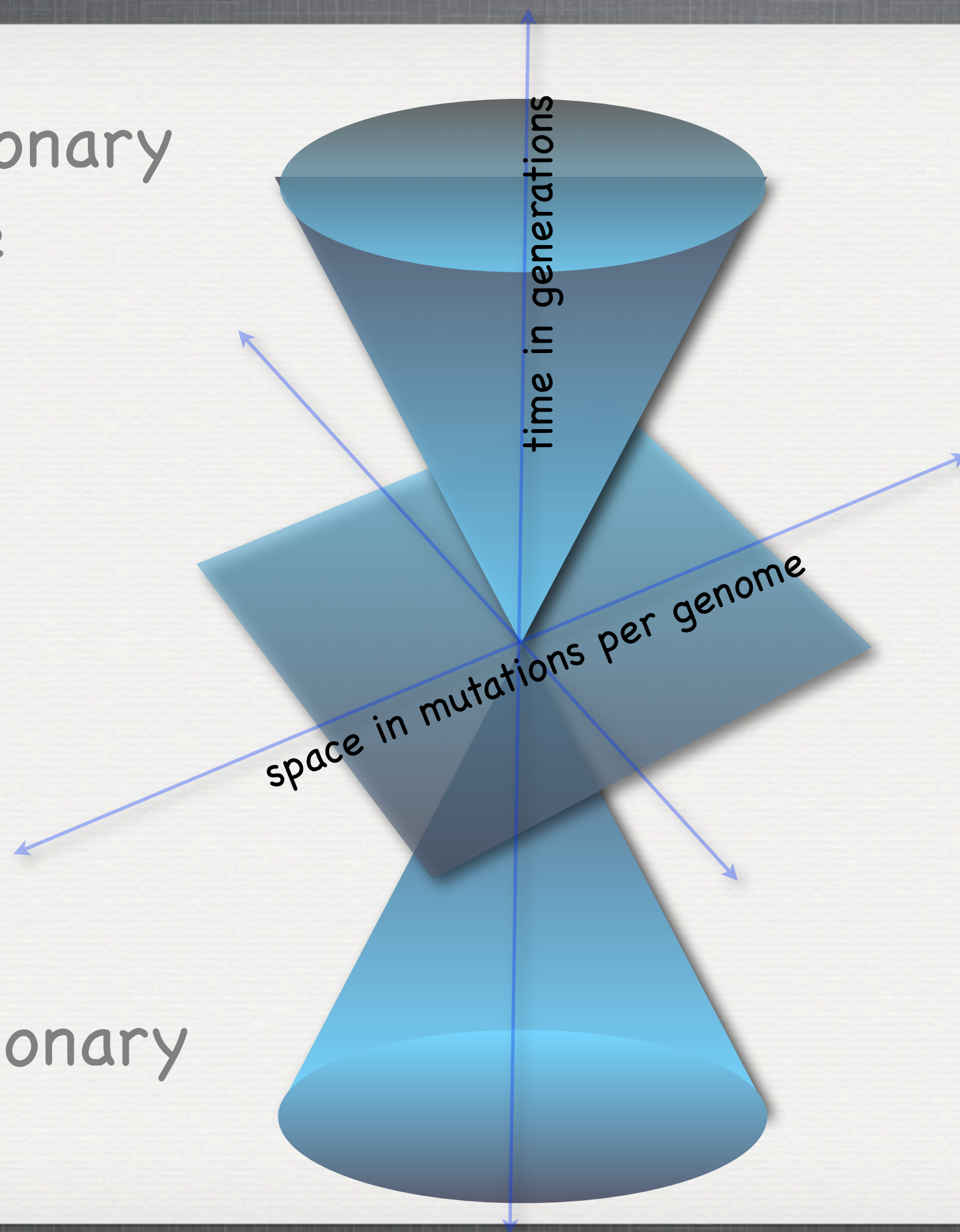
Max n subject to preserving g_i in the locally stable equilibrium distribution

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

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

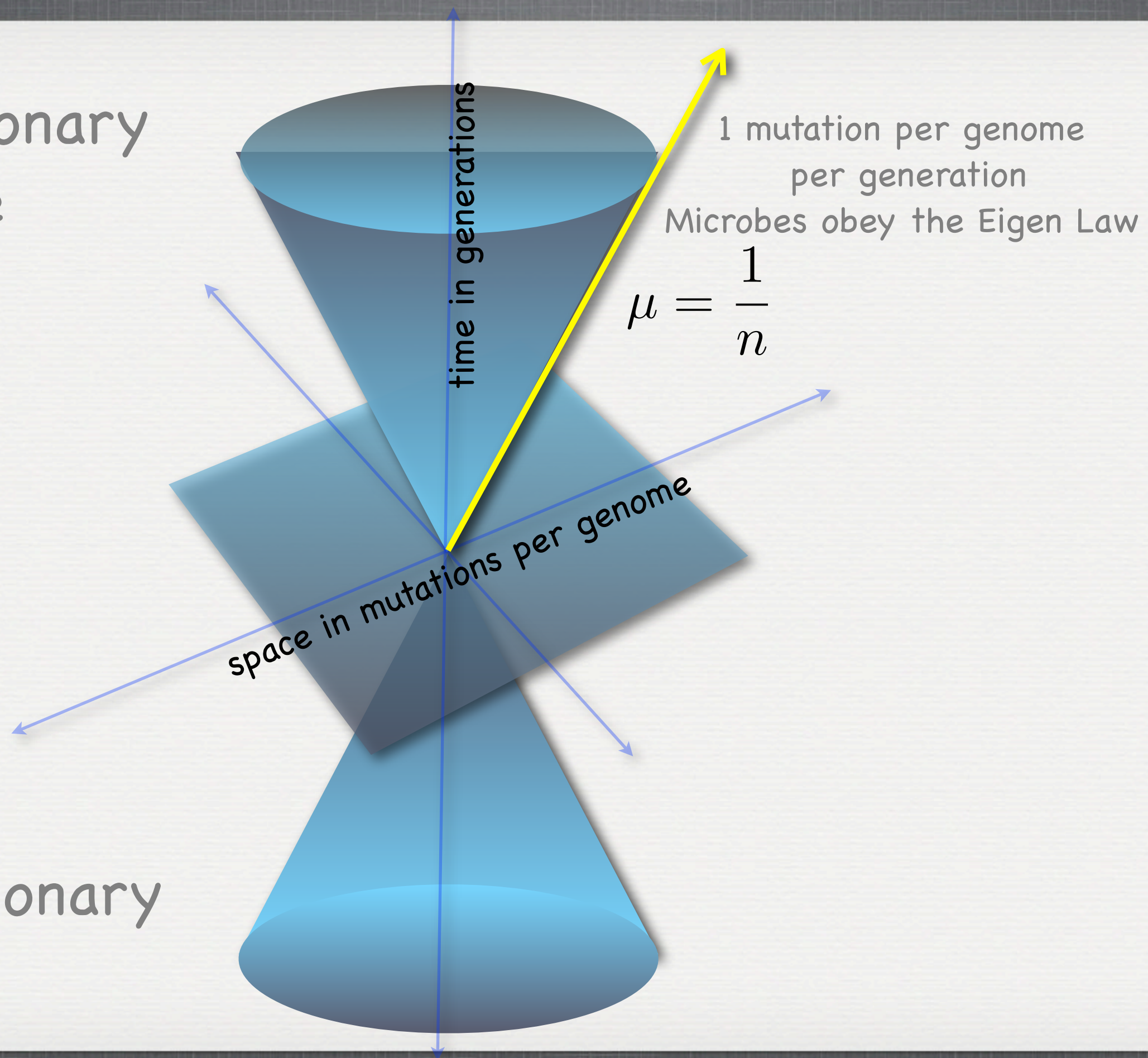


The evolutionary
future



The evolutionary
past

The evolutionary
future



The evolutionary
past

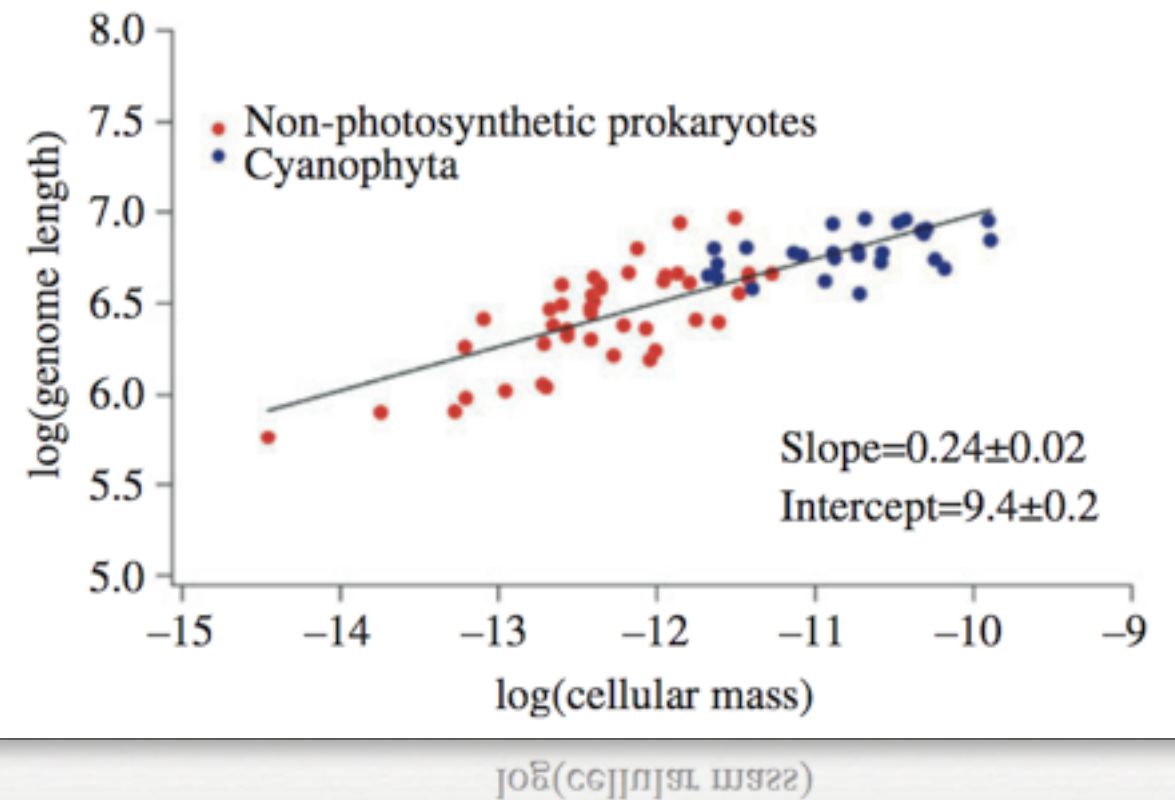
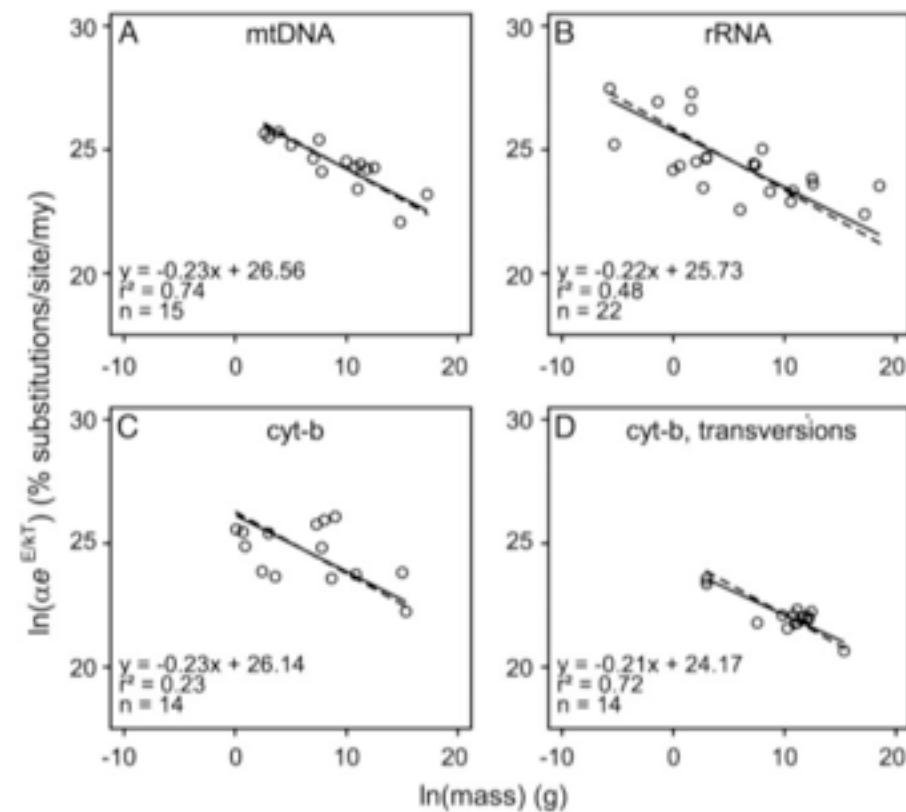
Testing the Prediction:

$$n = \frac{1}{\mu}$$

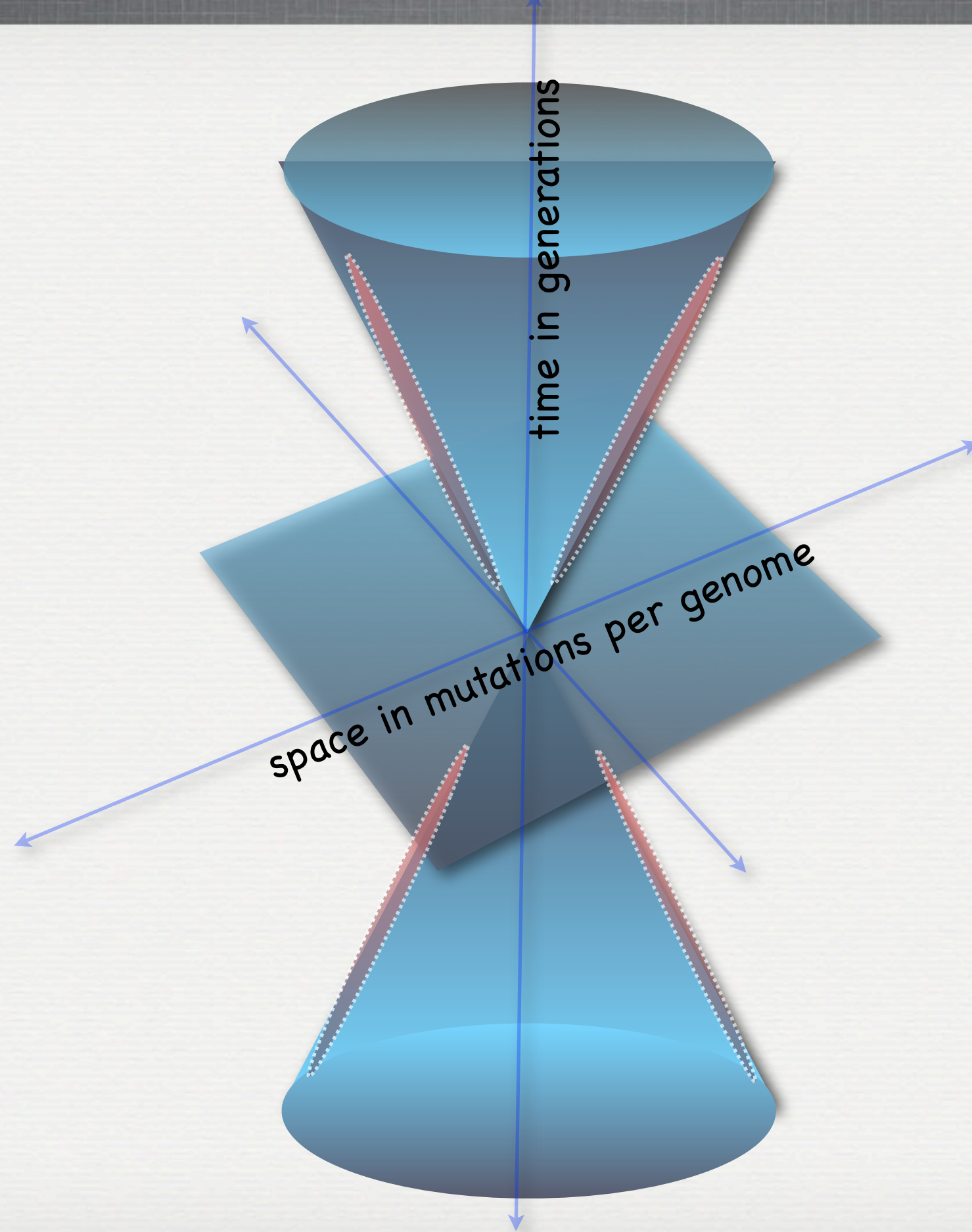
Evol. Maximization
metabolic constraint

$$\mu = km^{-\frac{1}{4}}$$

$$n = km^{\frac{1}{4}}$$



Prokaryotic life
evolves on the
membrane of life
cone



Evolutionary dynamics in microbes is extracting adaptive information
at the maximum possible velocity

Selection as Statistical Inference

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

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

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

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

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

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

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

Selection as Learning: (Imitation & Operant)

Biological Complexity is the mechanical / inferential support
for making more accurate hypotheses
about an expanding number of environmental regularities

But Evolutionary Light Speed Constrains the Maximum Rate of Inference

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

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

Insights from Page, Sigmund & others

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

$$g_i \longrightarrow p_i \qquad \sum_i g_i(t=0) = 1 \qquad \bar{r} = \sum_i r_i g_i$$

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

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

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

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

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

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

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

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

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

The Price Equation

Uses of Price Equation

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

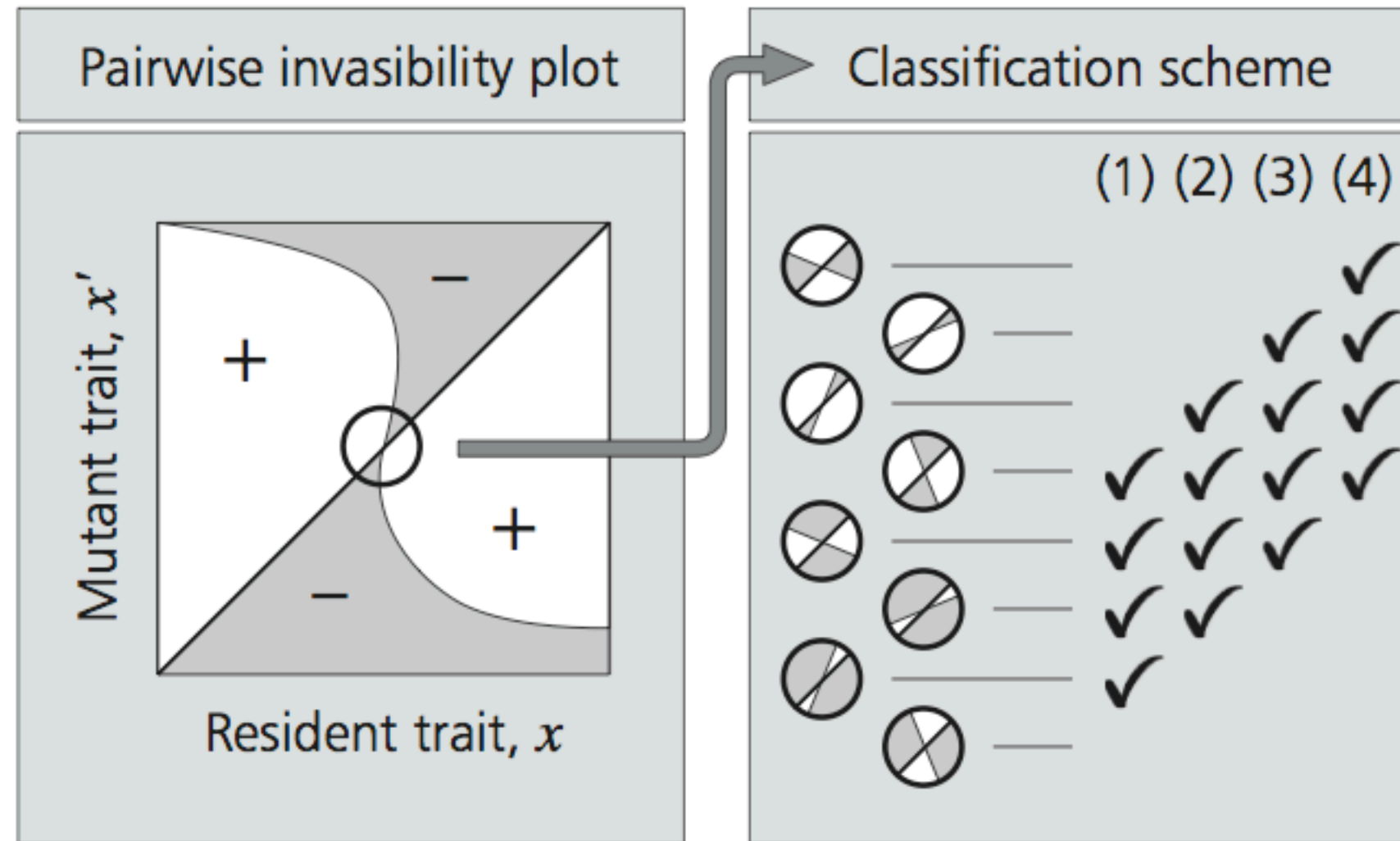


Phenotypic Evolution

Deriving Adaptive Dynamics

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

Evolutionary Game Adaptive Dynamics for Continuous Traits



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

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

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

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

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

**Taylor
series**

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

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

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

$$\dot{E}[p] = Var(p) \frac{\partial r(a, g)}{\partial a} \Big|_{a=\bar{p}}$$

Conclusions I.

- Simple stoichiometry allows us to derive many of the fundamental equations of evolutionary dynamics
- How genomes change in frequency as a result of frequency-dependence, density dependence and mutation.
- These equations provide insights into how total genomic information is constrained by mutation rates - Eigen law
- Allow us to study game dynamics in an evolutionary and ecological framework
- Through AD & Price Eq. provide the basis for many current studies on cooperation, kin & group selection, microbial dynamics and cultural/language evolution.

Select Bibliography

Advanced

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

Intermediate

- Kimura, M. The Neutral Theory of Molecular Evolution. (1983)
- Eigen, M. . "Self-organization of matter and evolution of biological Macromolecules". Naturwissenschaften 58 (10): 465. (1971)
- Price, G.R. . "Selection and covariance". Nature 227: 520–521. (1970)

Advanced

- Jaynes, E.T. Probability Theory: The Logic of Science. (1998)

Intermediate

- Frank, S.A. . Foundations of Social Evolution. PUP. (1998)

Intro

- Nowak, Martin , Evolutionary Dynamics: Exploring the Equations of Life, Belknap Press. (2006)

Intermediate

- Rice. S. Evolutionary Theory: Mathematical and Conceptual Foundations. (2004)