Evolution: 1-3

- Foundations - *evolutionary dynamics*
- Phylogeny and Ontogeny - *evolution of development*
- Frontiers - *Demons, coevolution, niche construction and cultural change*

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 of organismal to ecological structure?
- What is the relationship of genetic information to learned information?
- When does cultural evolution outpace genetic evolution?

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.

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.

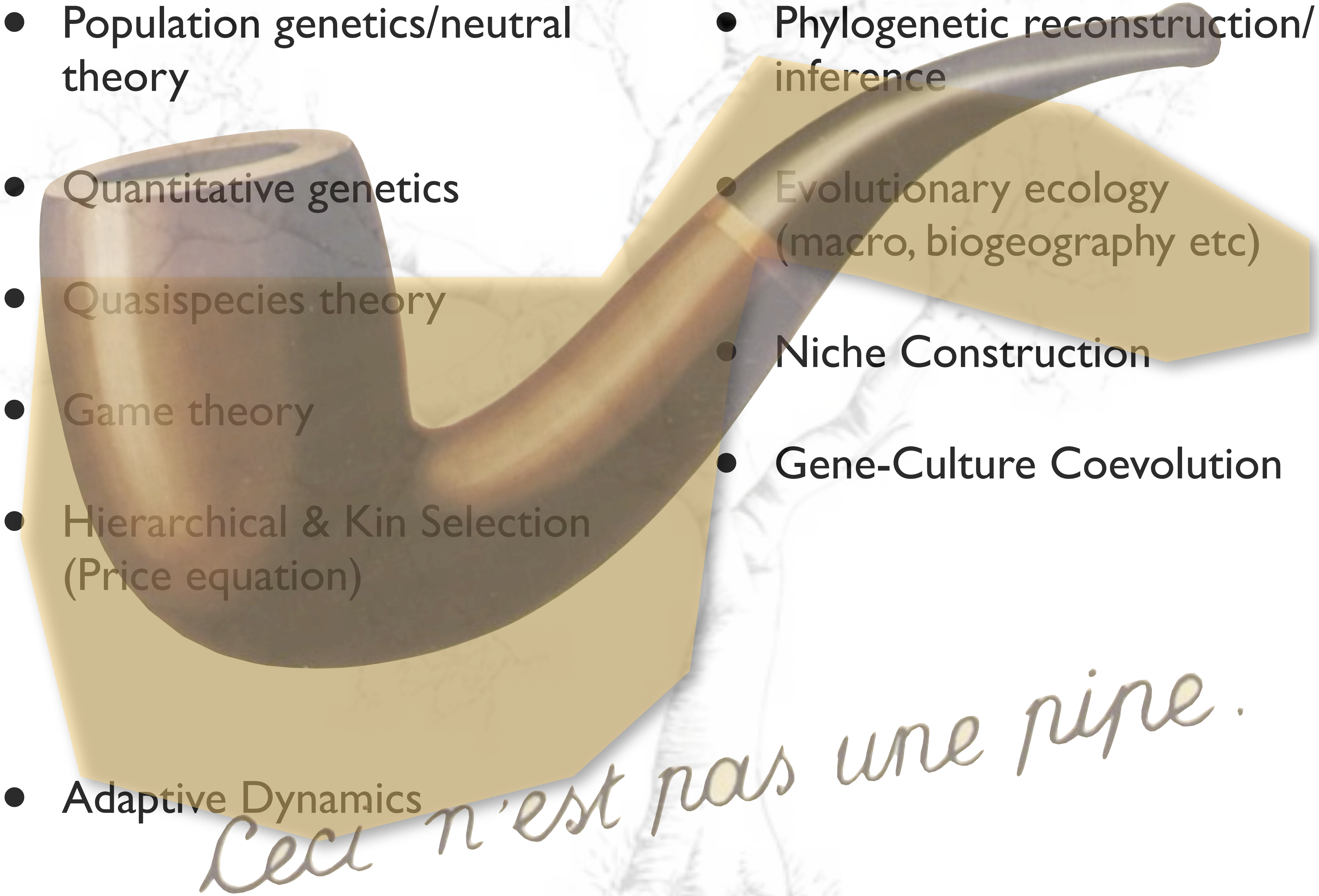
Assumptions :- pre-Darwinian

- 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
- Gene-Culture Coevolution



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

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

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

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

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

Evolutionary Stoichiometry

Development

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

Typically Treated Thus

$$g_i \xrightarrow{d_i} p_i$$

Replicator Equation

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

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

$$n \quad \text{genomes}$$

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

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

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

Evolutionary Game Theory: Frequency dependent Replicator Equation

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

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

$$n \quad \text{genomes}$$

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

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

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

$$\dot{g}_i = g_i\Big(\sum_{j}^{n} g_j p_{ij} - \sum_{j}^{n} g_j \sum_{k}^{n} g_k p_{jk}\Big)$$

Stable Equilibria of Replicator Eq. and Nash Equilibria

Mathematica Demo

Freq-dep Replicator Equation & Bayesian Inference

An Insight by Cosma Shalizi

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

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

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

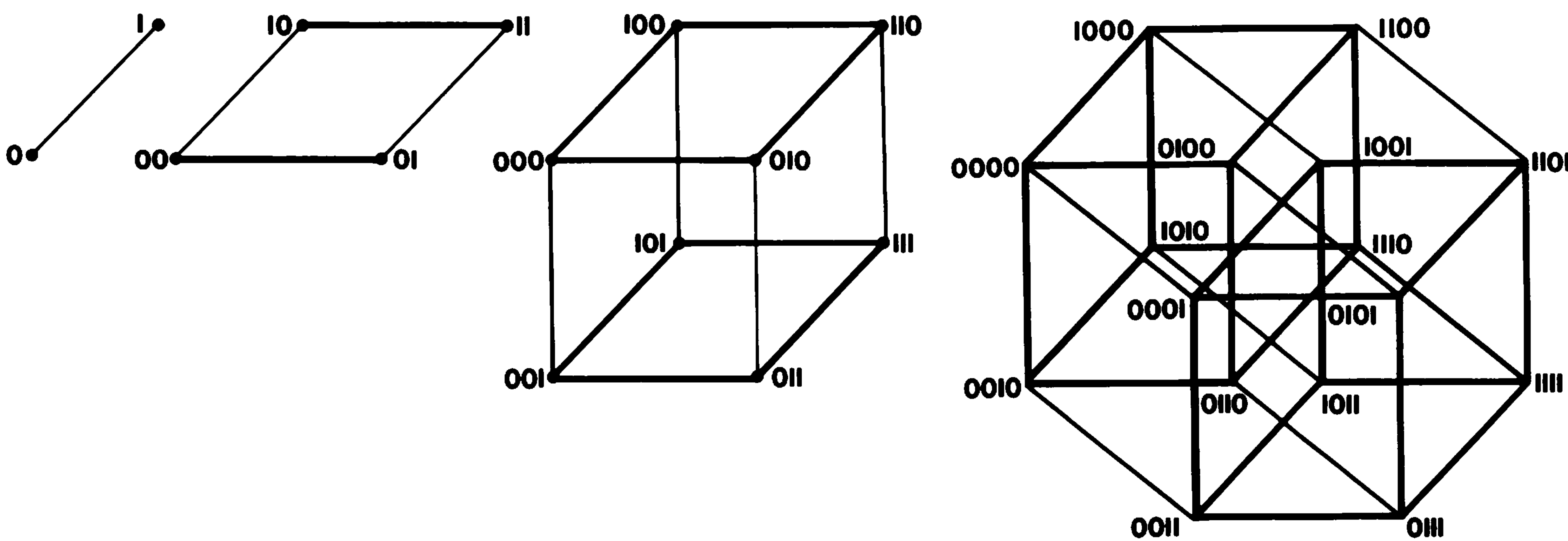
$$\bar{L} = P(Y) = \sum_{x \in \omega} P(Y|X)P(X)$$

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

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

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

Mutation & Sequence Space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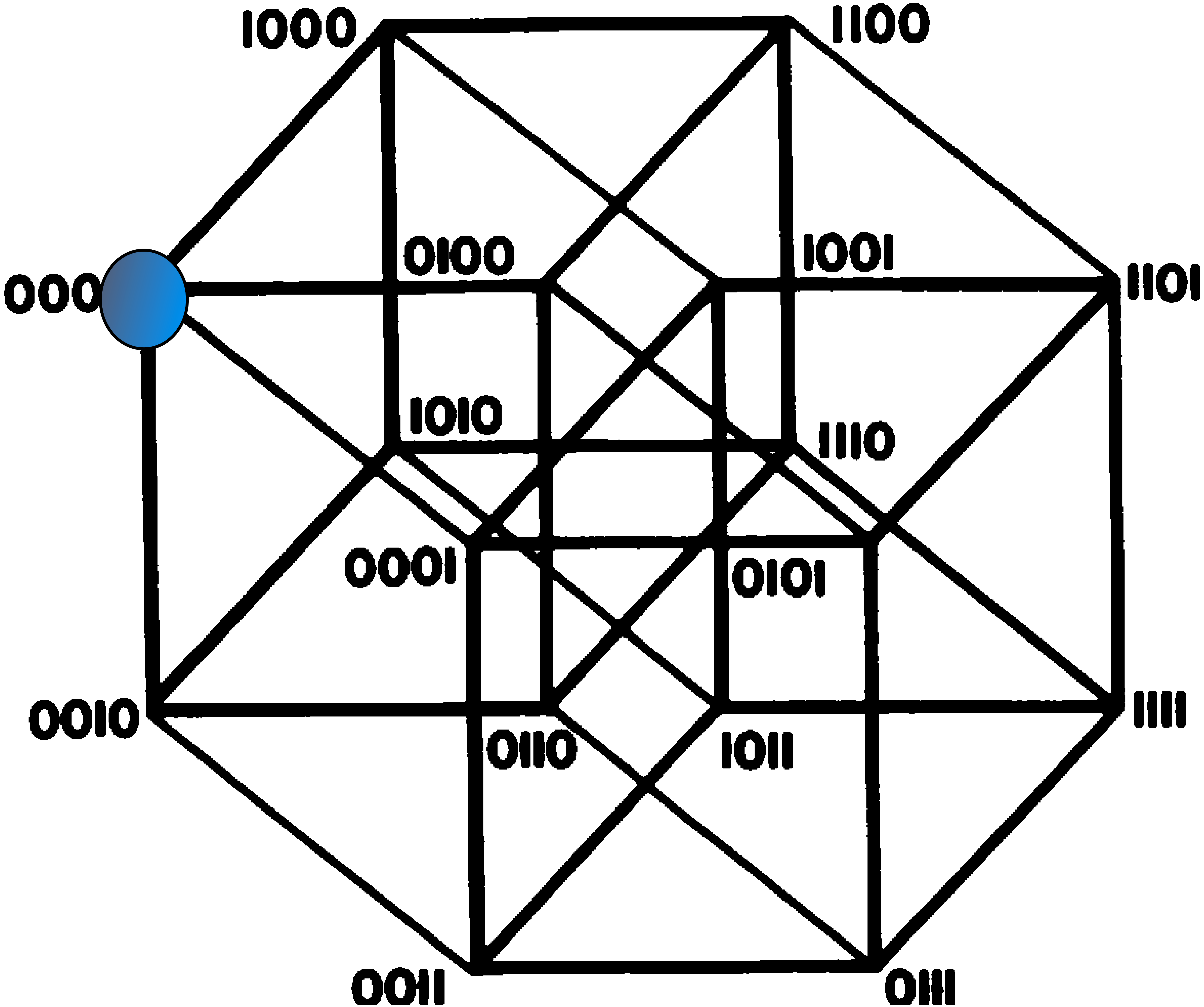
Replicator-Mutator Equation

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

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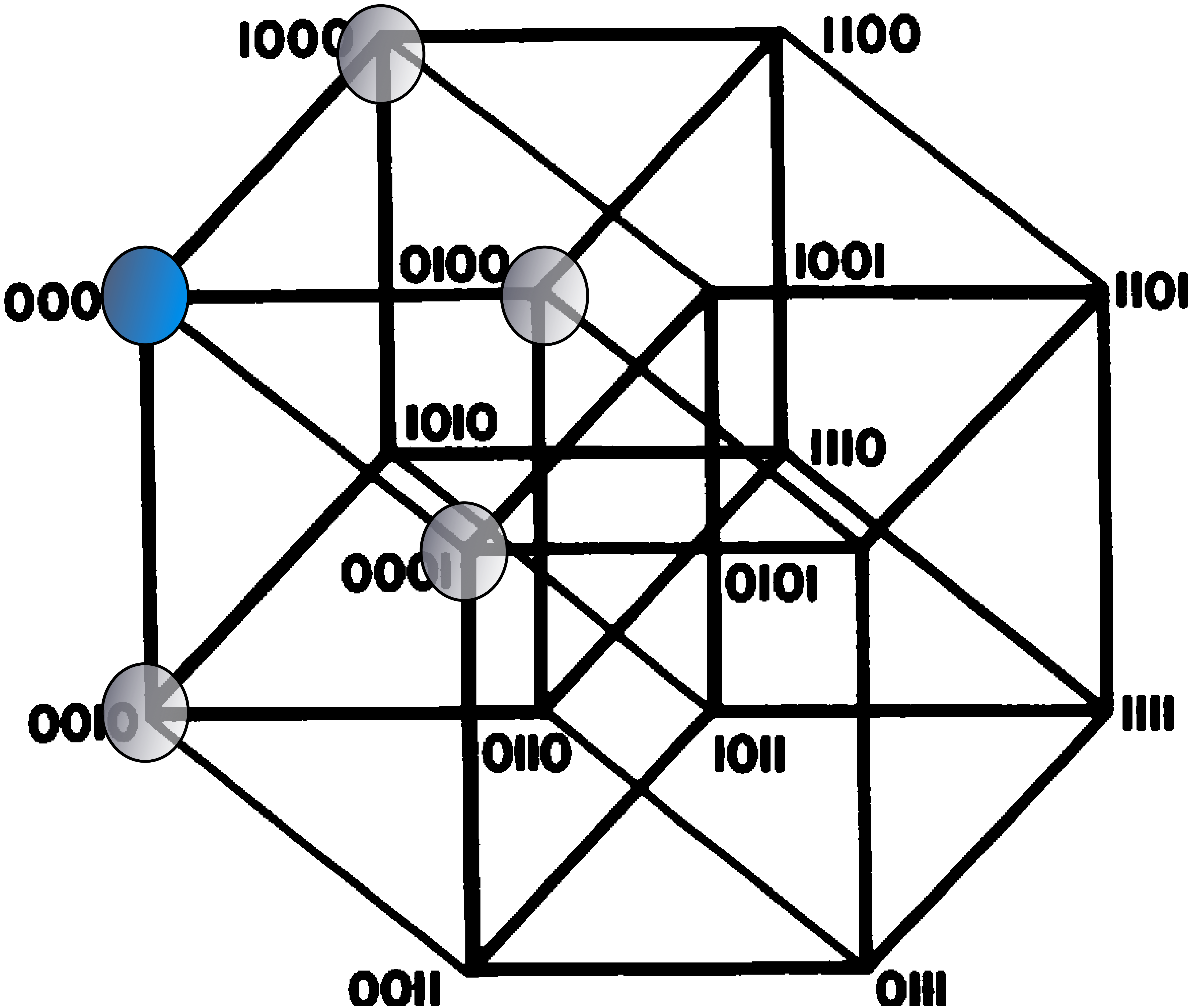

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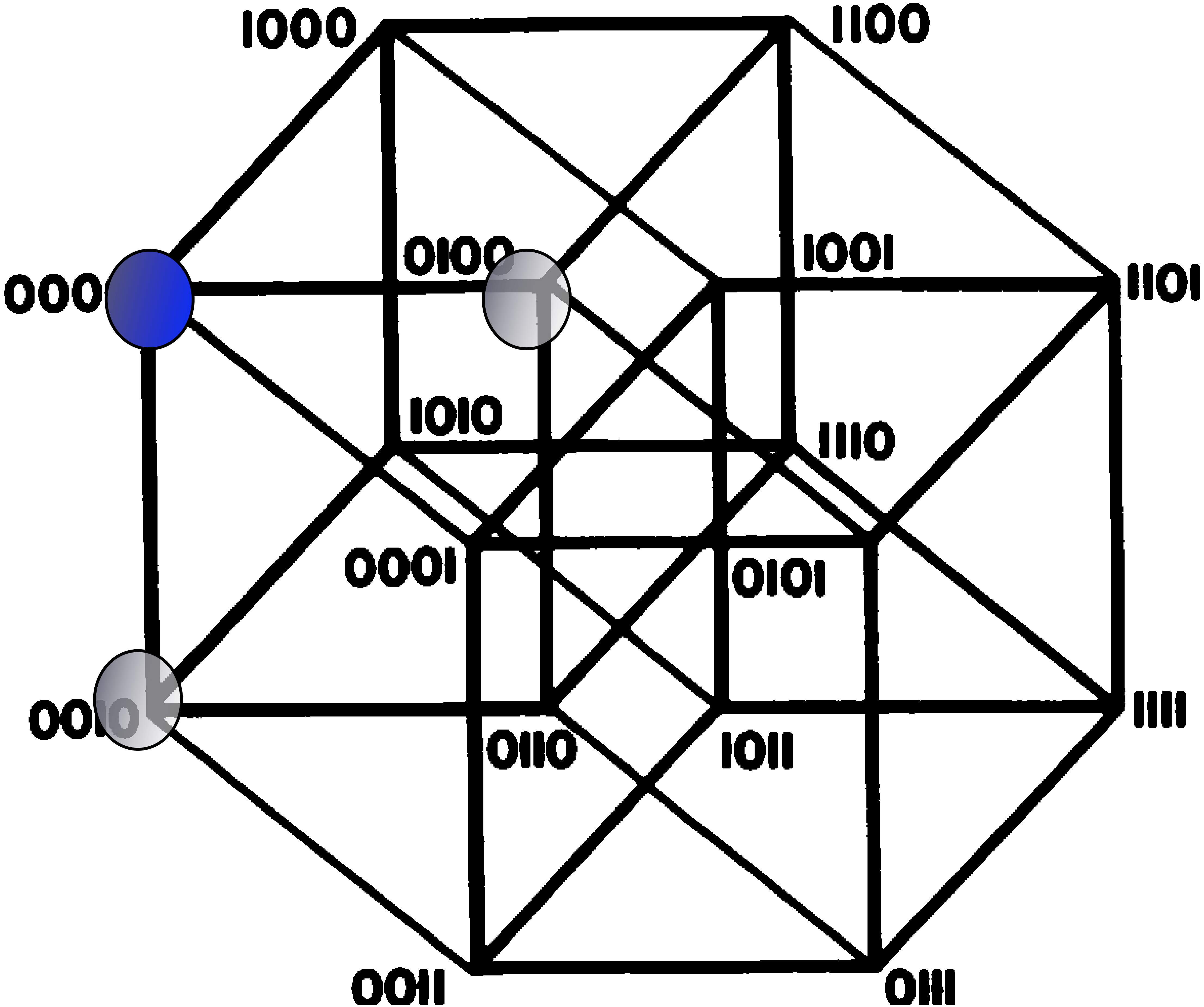
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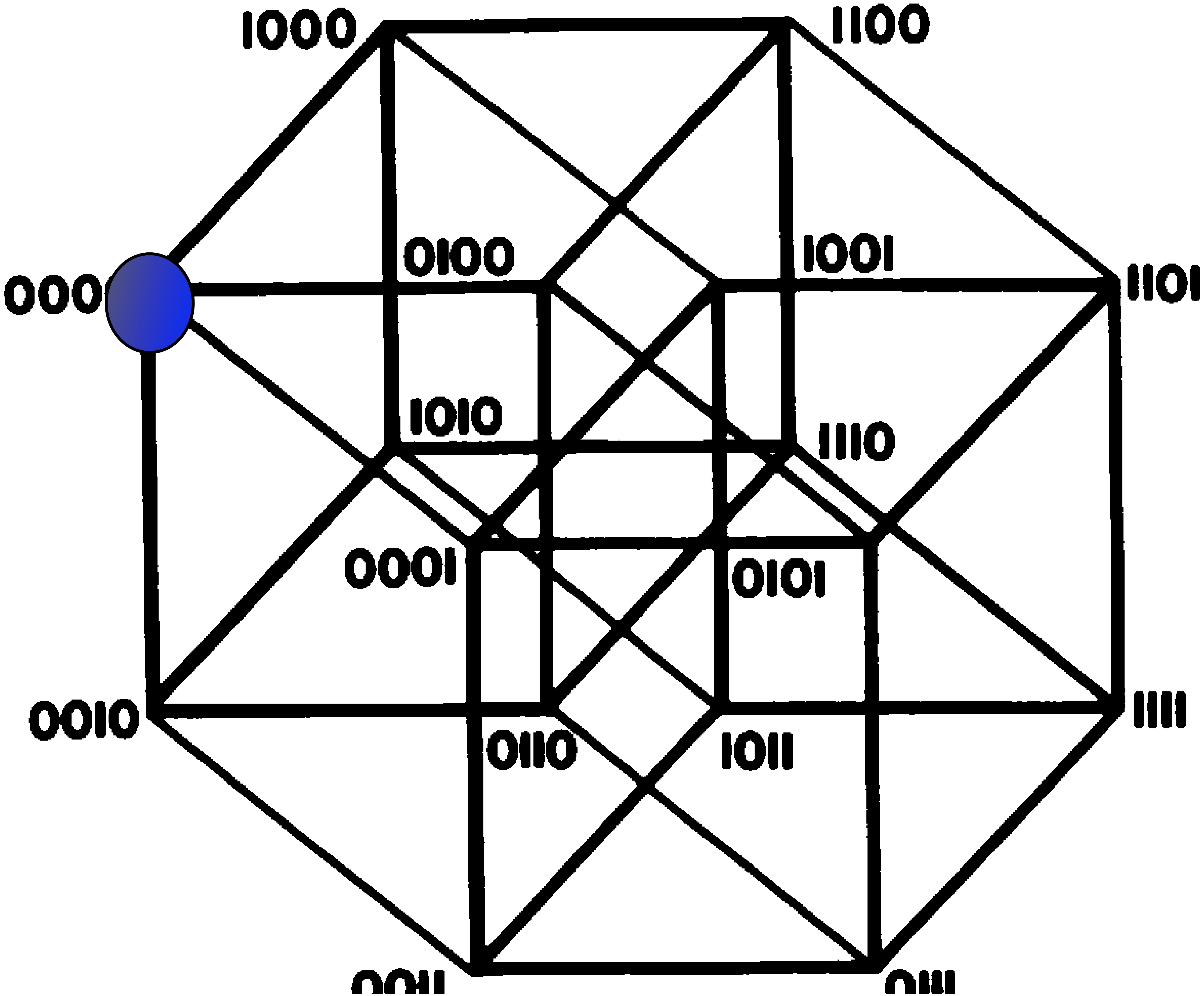
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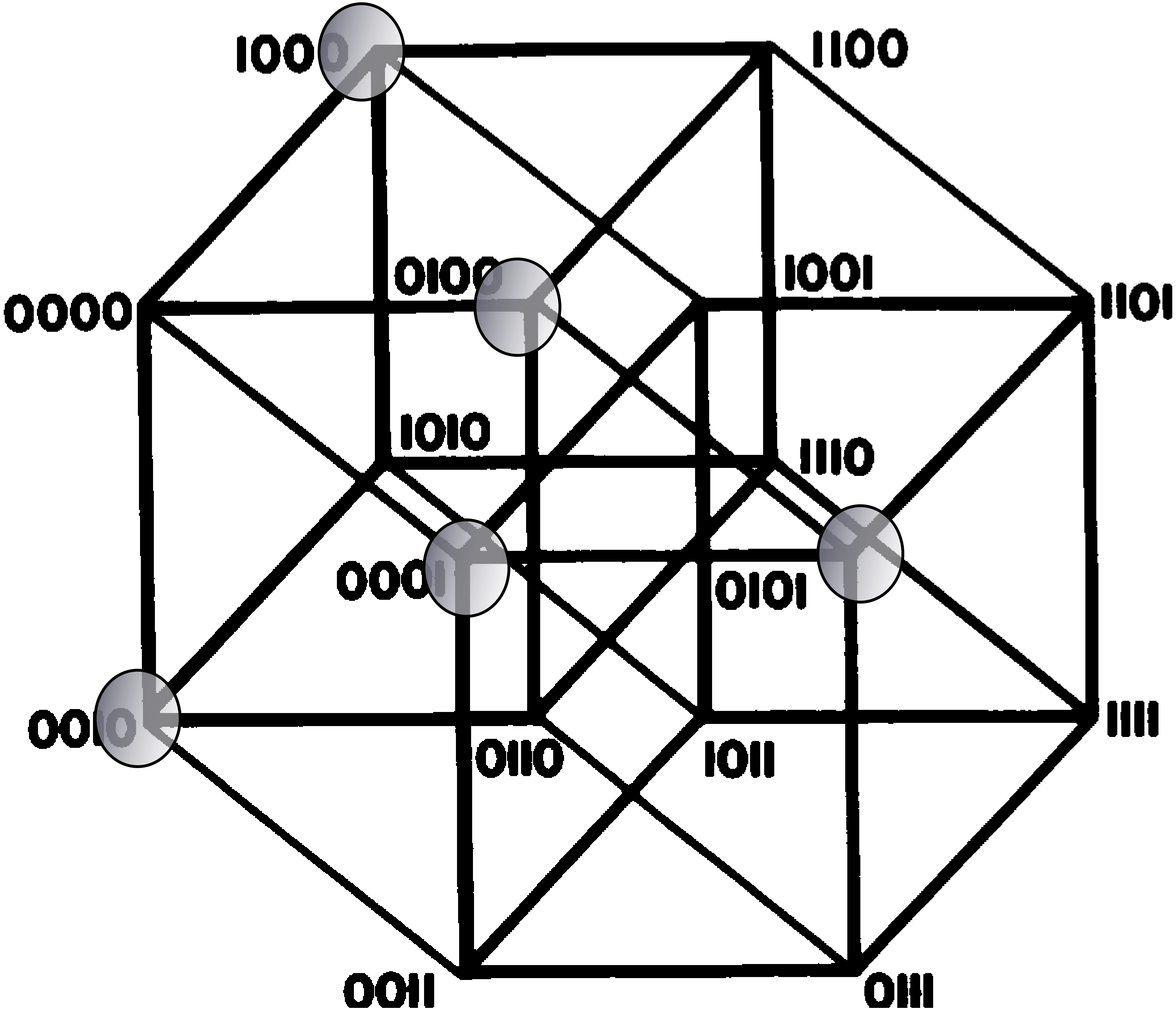
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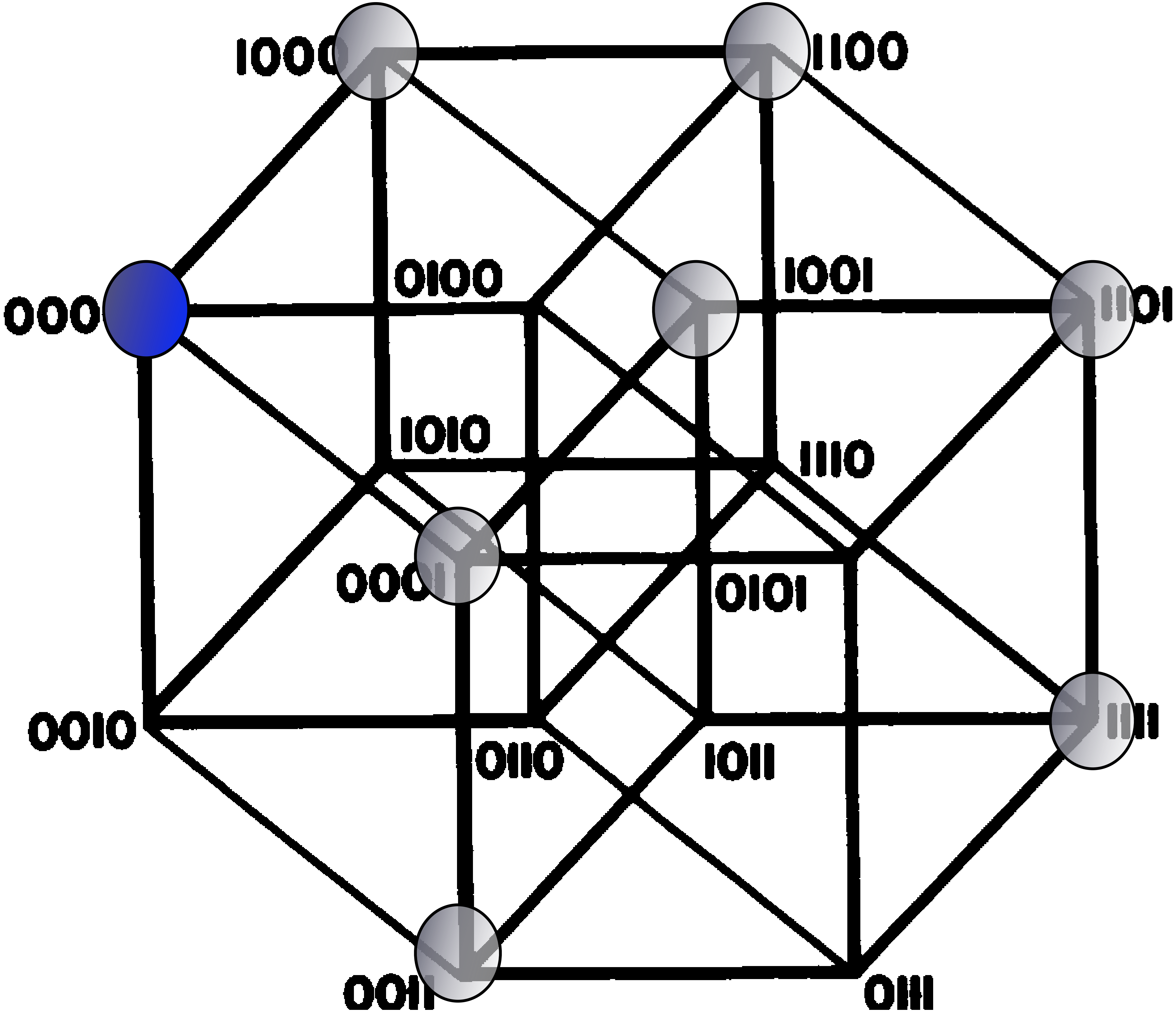
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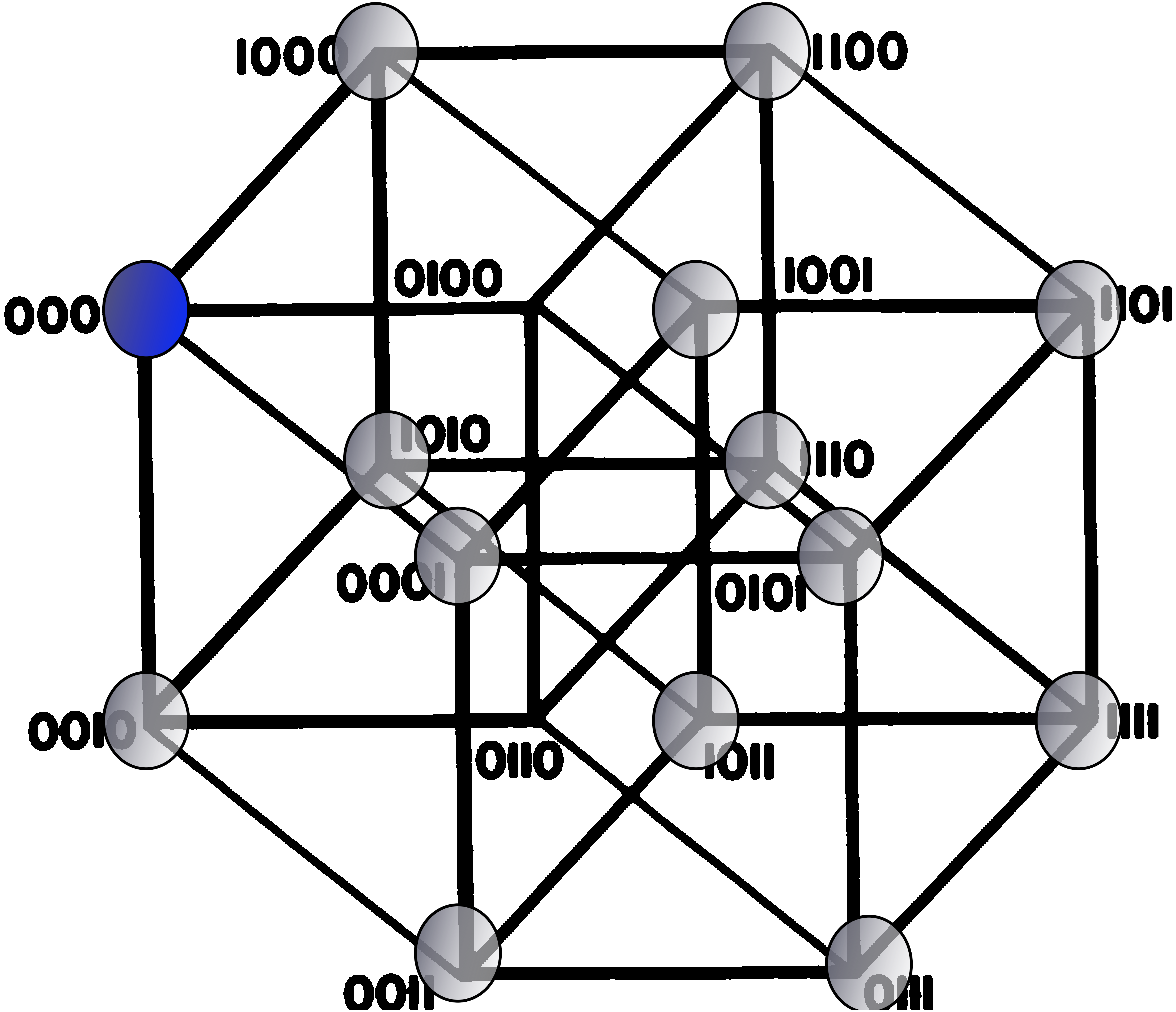

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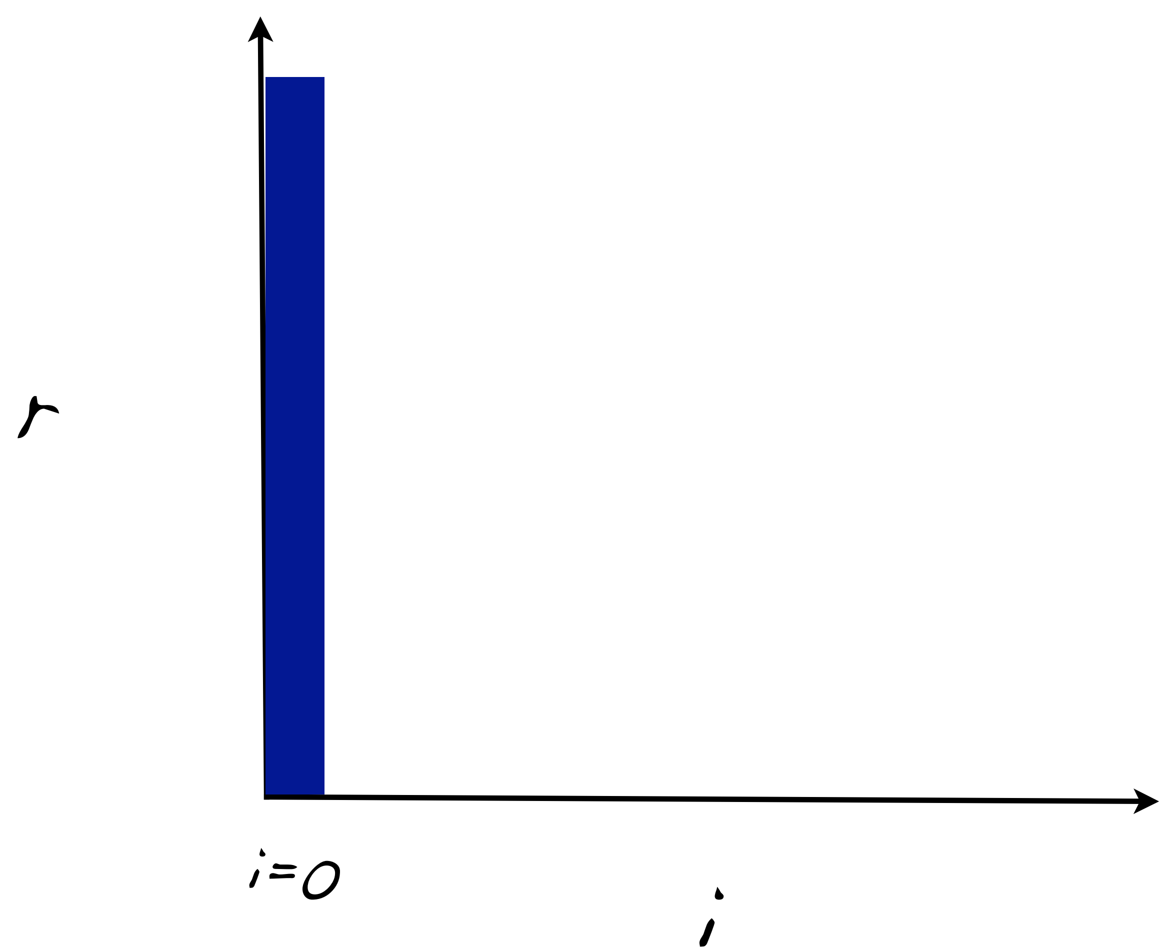
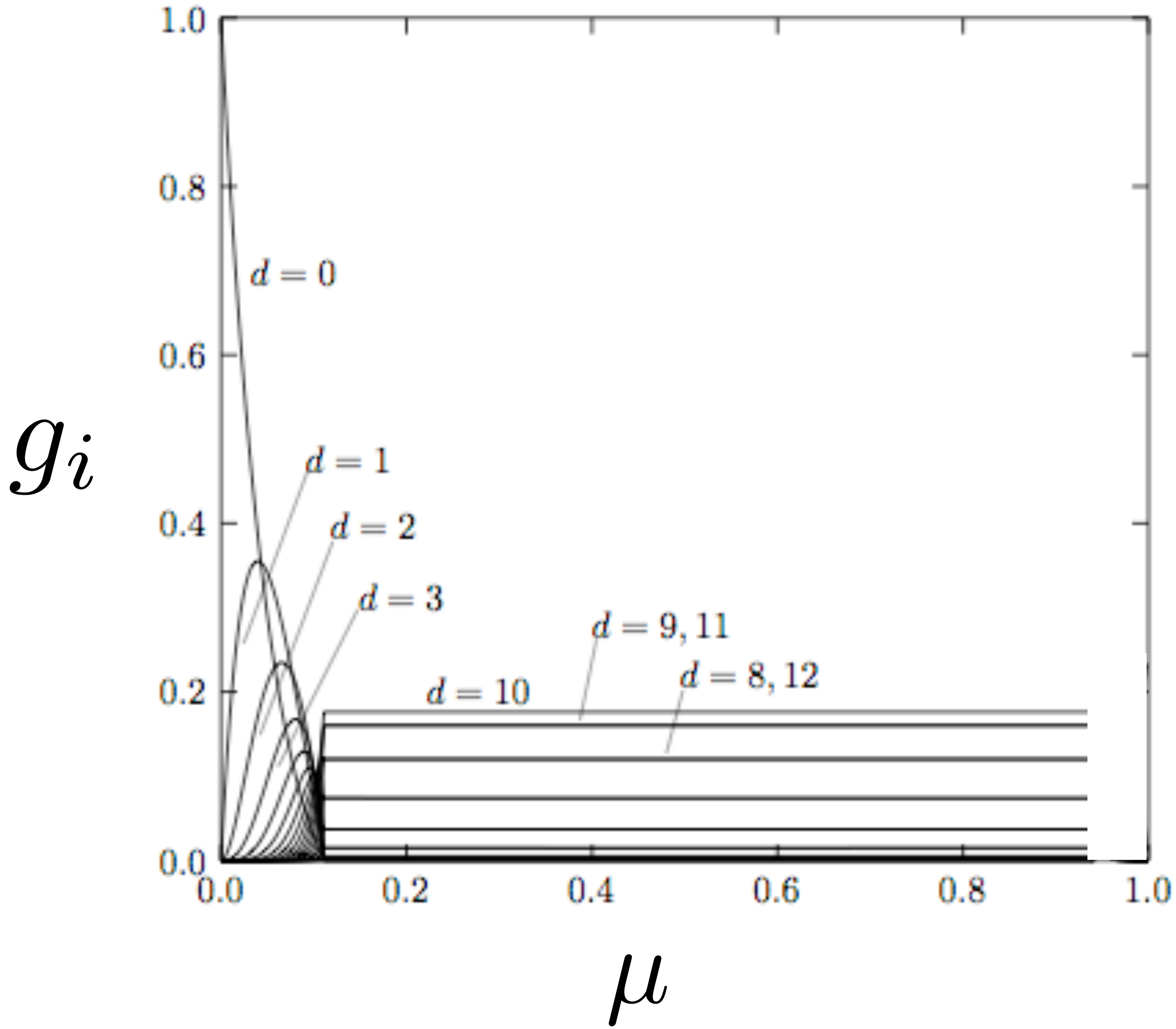
Delta-function landscape



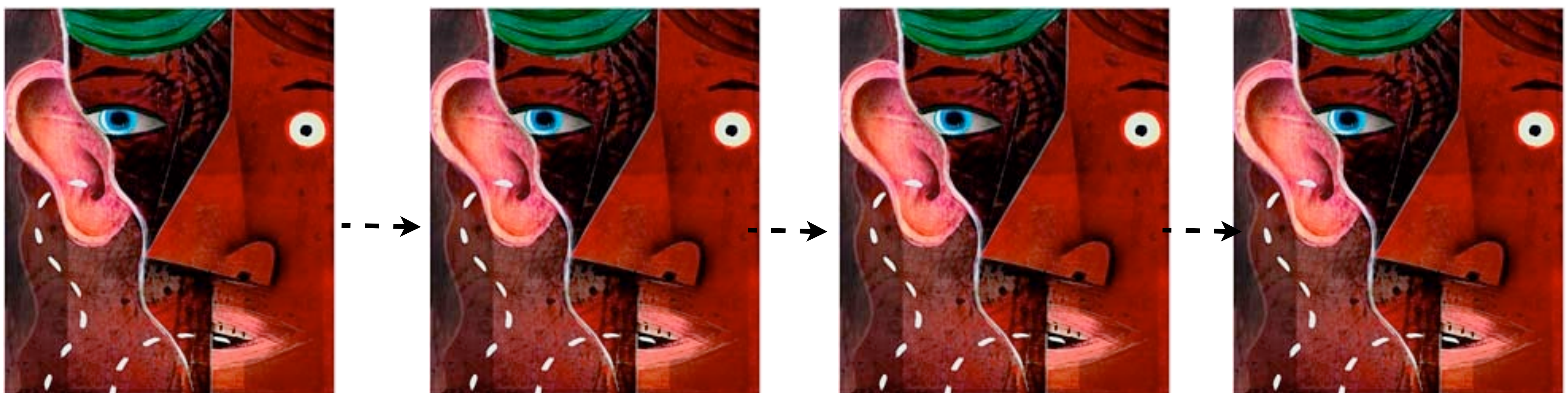
Error Threshold



Error Threshold

Delta function:

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



μ μ μ

$L = 1$ $L = 2$ $L = 3$ $L = 4$

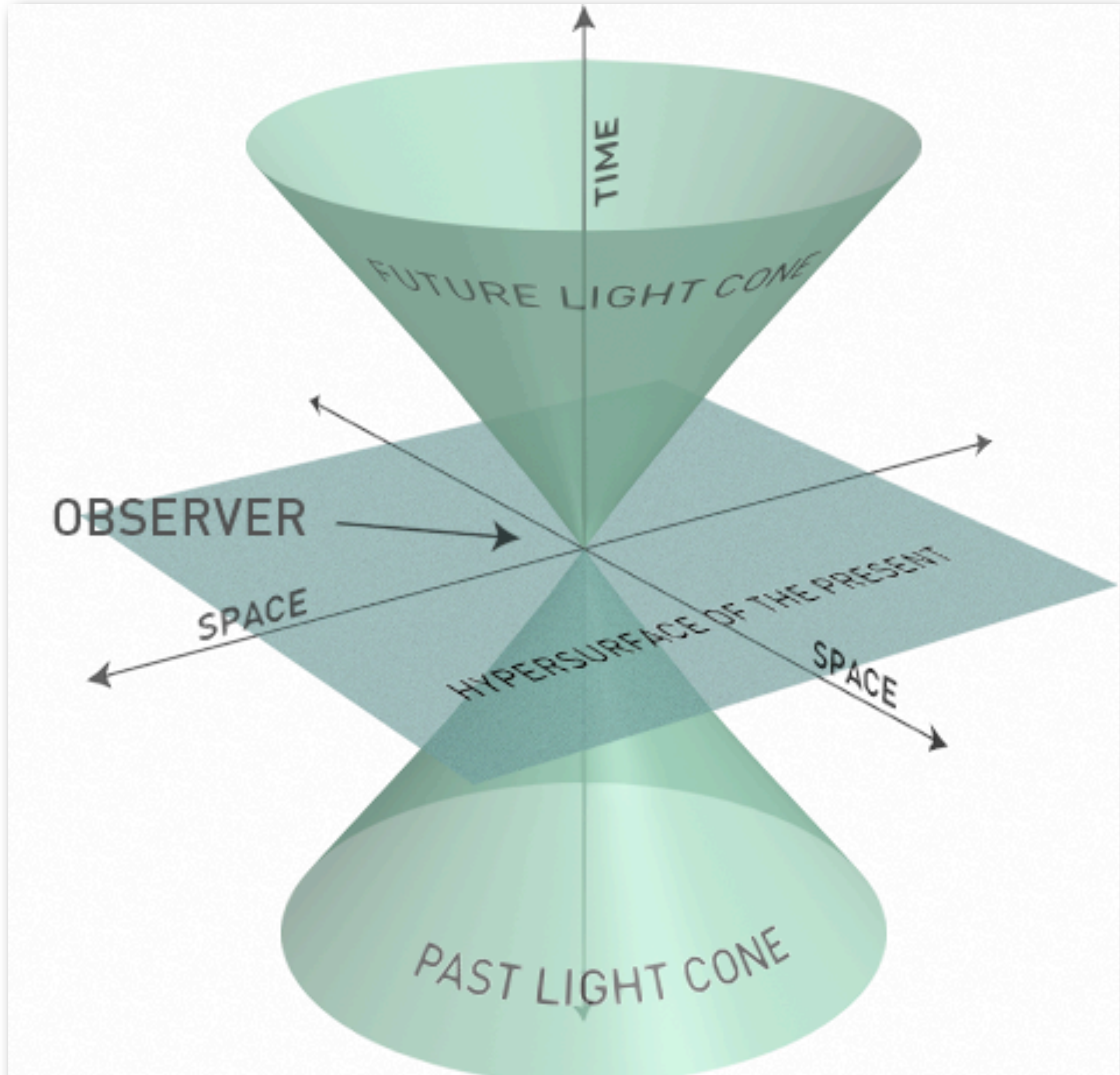
Fitness Landscape

Delta function:

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

Multiplicative function:

$$\mu < s$$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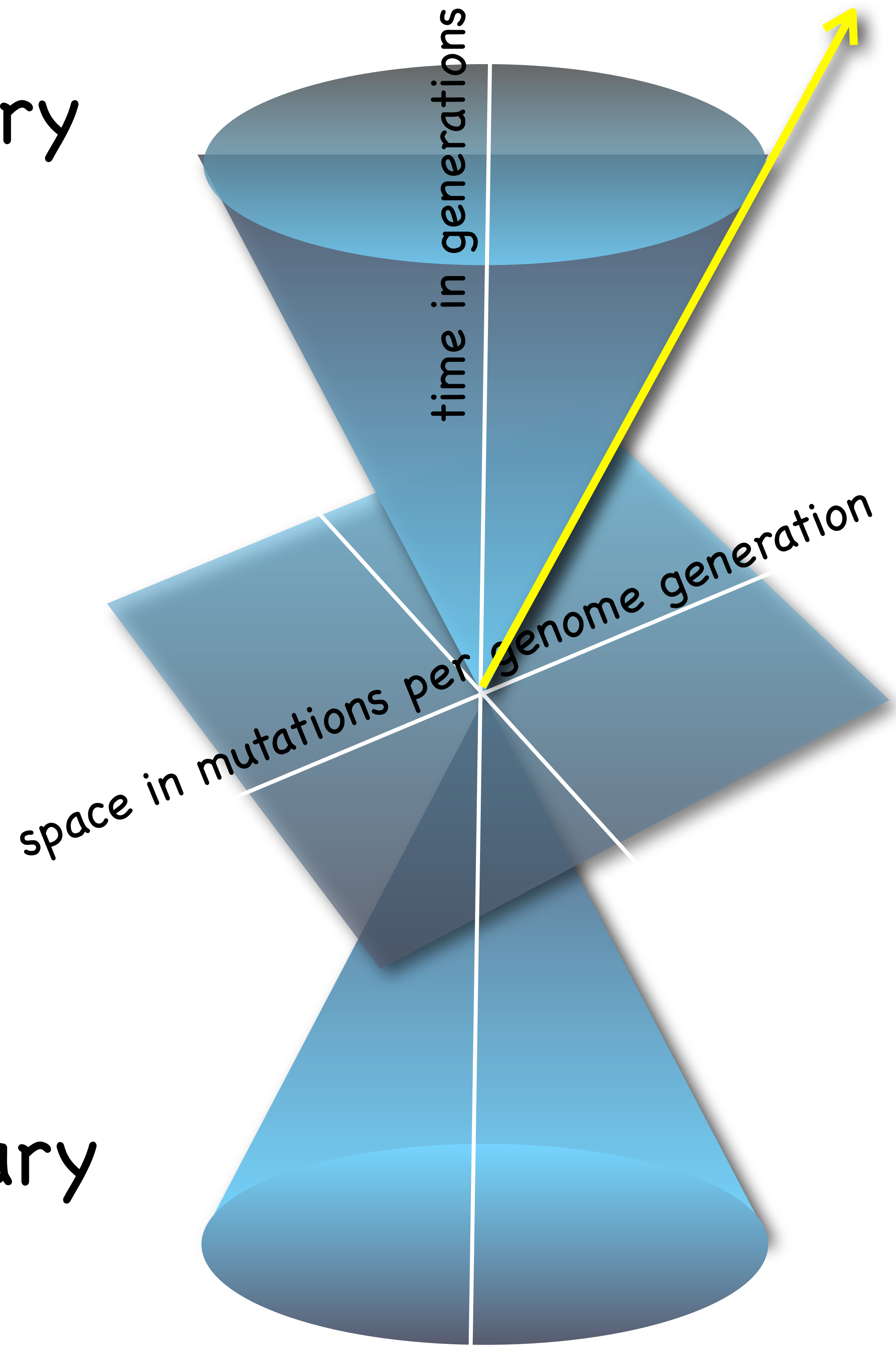
HYPERSURFACE OF THE PRESENT
SPACE
PAST LIGHT CONE

The evolutionary future

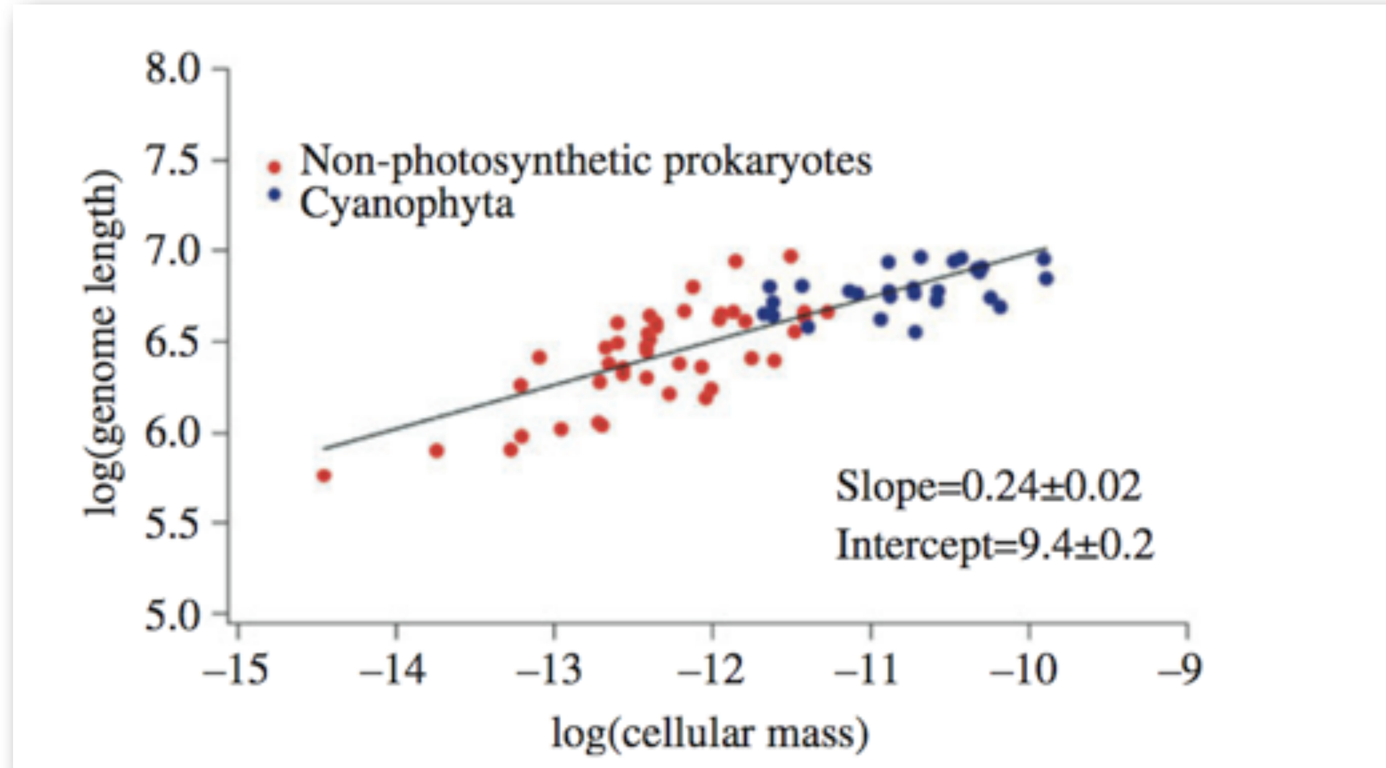


1 mutation per genome per generation = The Eigen Law

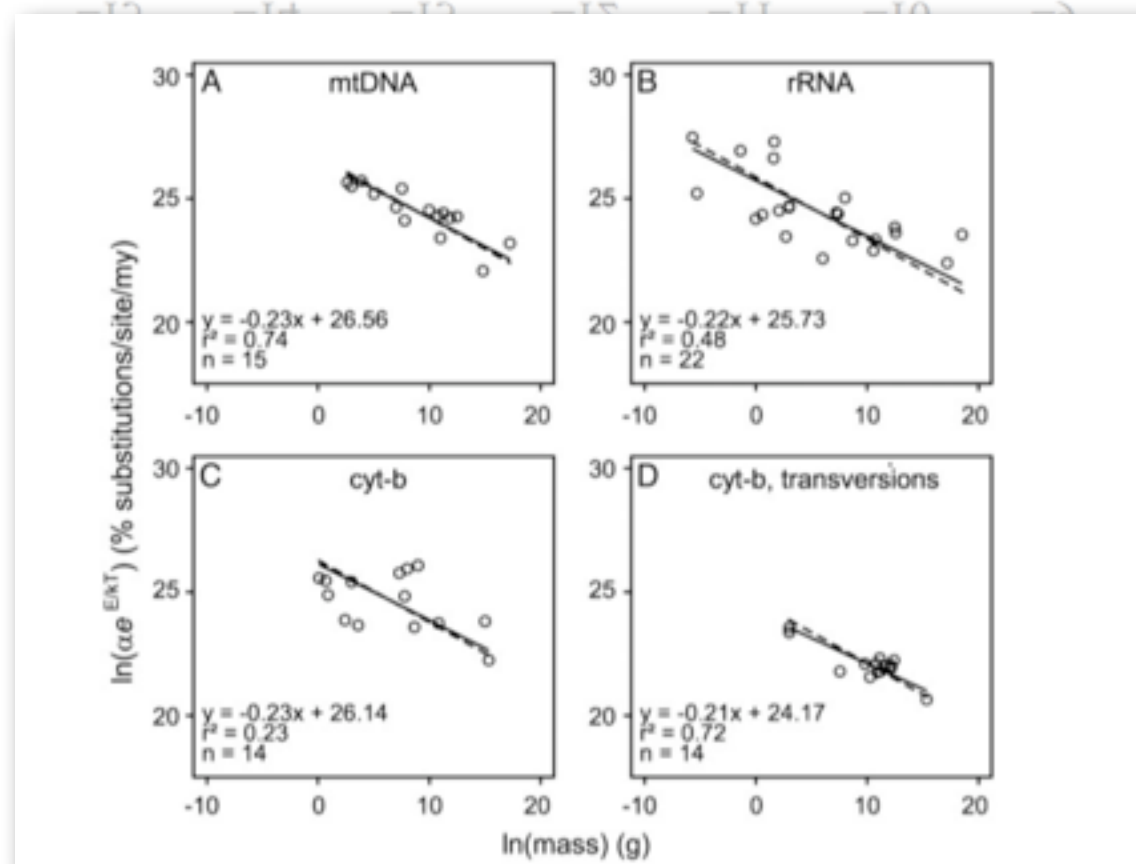
$$\mu = \frac{1}{L}$$

The evolutionary past

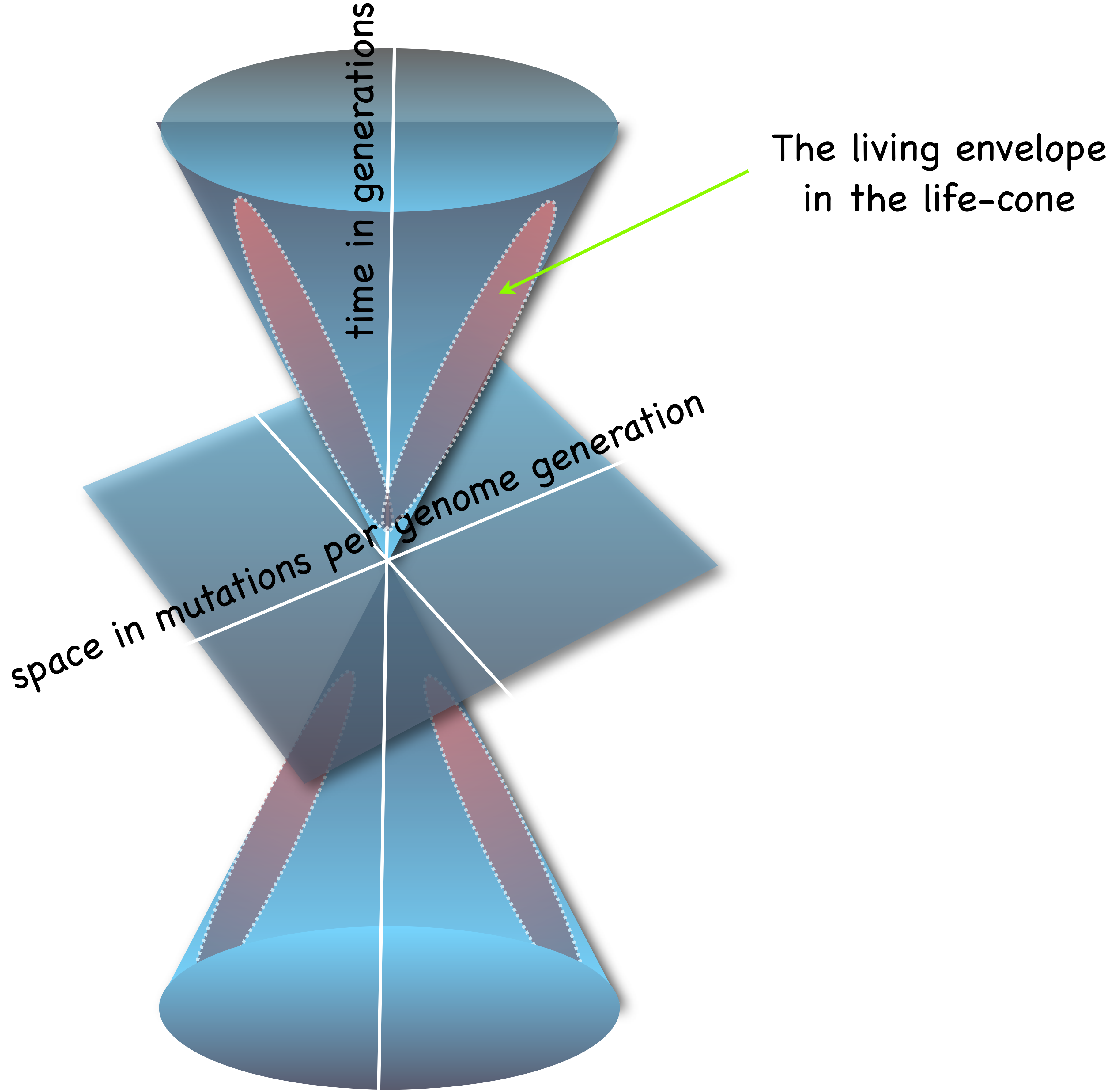
$$L = km^{\frac{1}{4}}$$



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



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


time in generations
The living envelope
in the life-cone
space in mutations per genome generation

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

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

Insights from Page, Sigmund & others

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

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

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

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

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

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

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

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

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

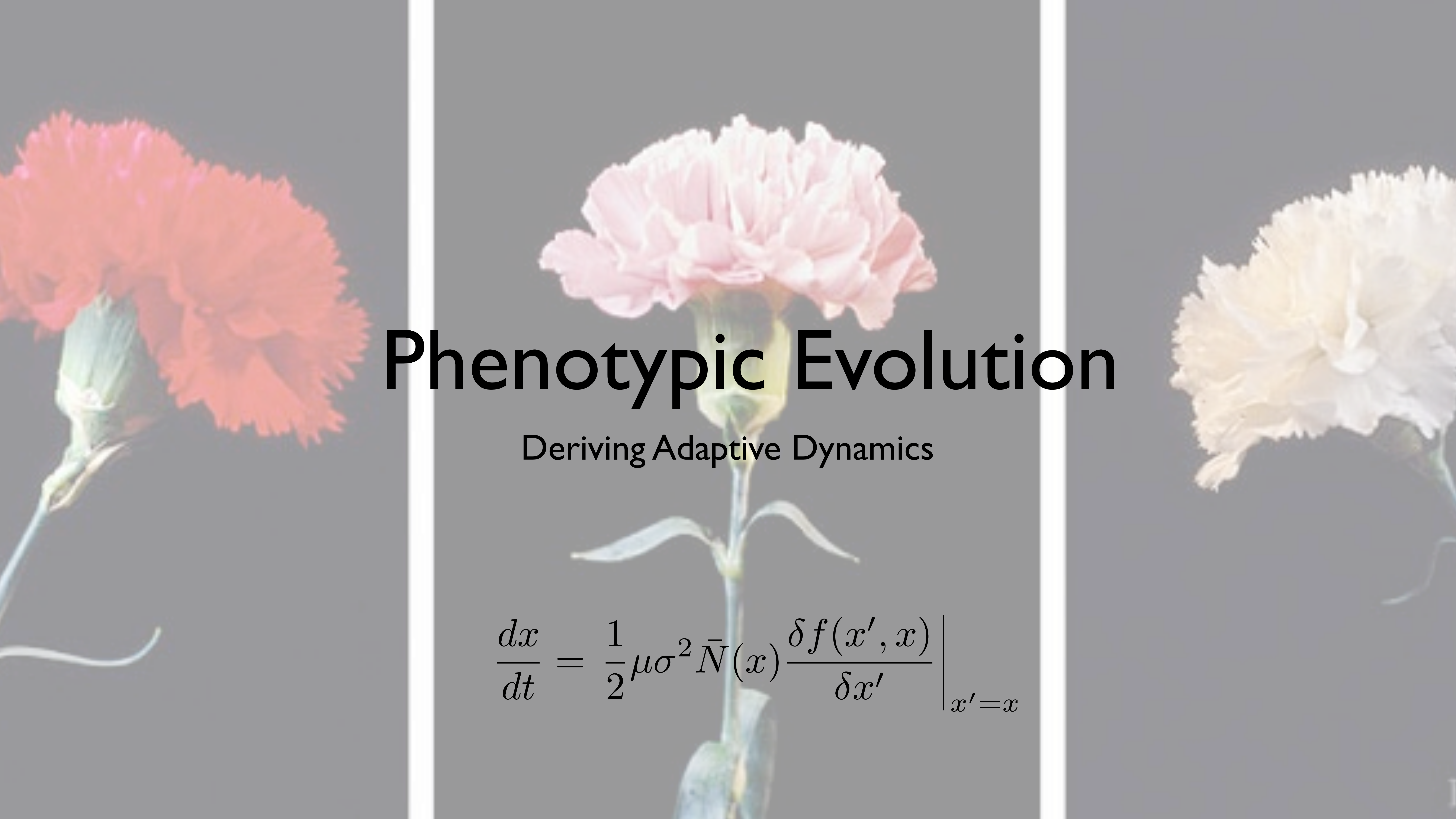
$$E[r\Delta_m p] = \sum_j g_j r_j \sum_i m_{ji}(p_i - p_j)$$

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

The Price Equation

Uses of Price Equation

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

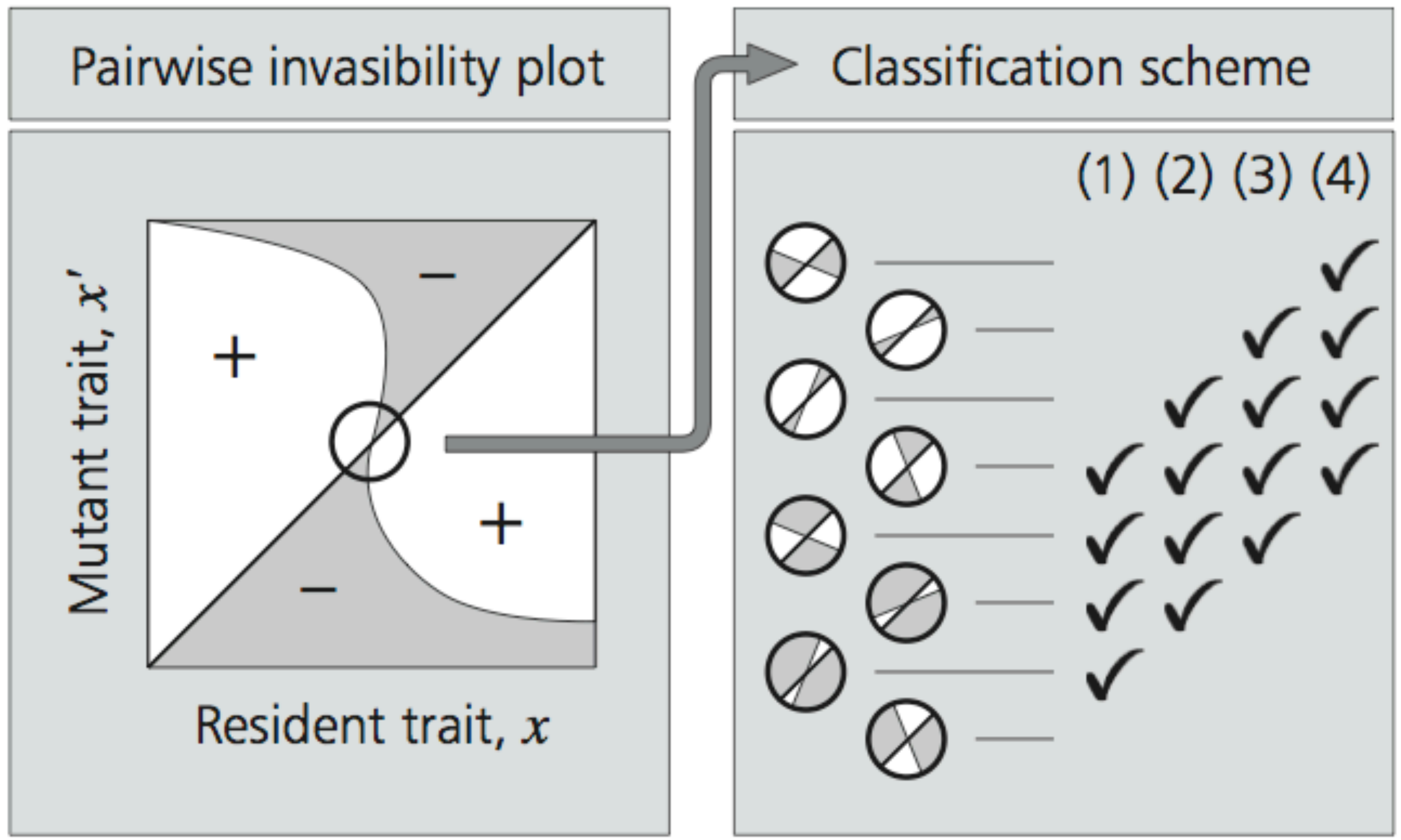


Phenotypic Evolution

Deriving Adaptive Dynamics

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

Evolutionary Game Adaptive Dynamics for Continuous Traits



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

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

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

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

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

Taylor series

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

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

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

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

Conclusions 1.

- 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.

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