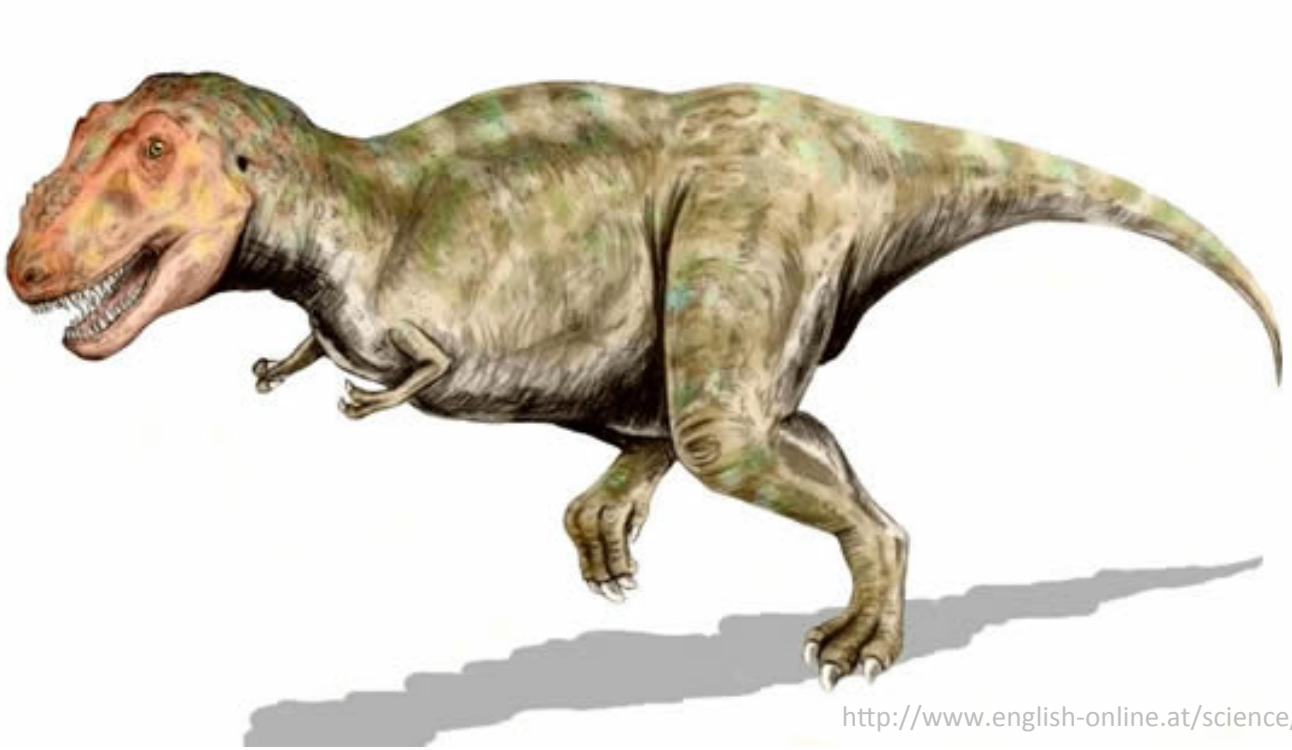
# *T. rex.*

http://www.english-online.at/science/dinosaurs/tyrannosaurus-rex.jpg

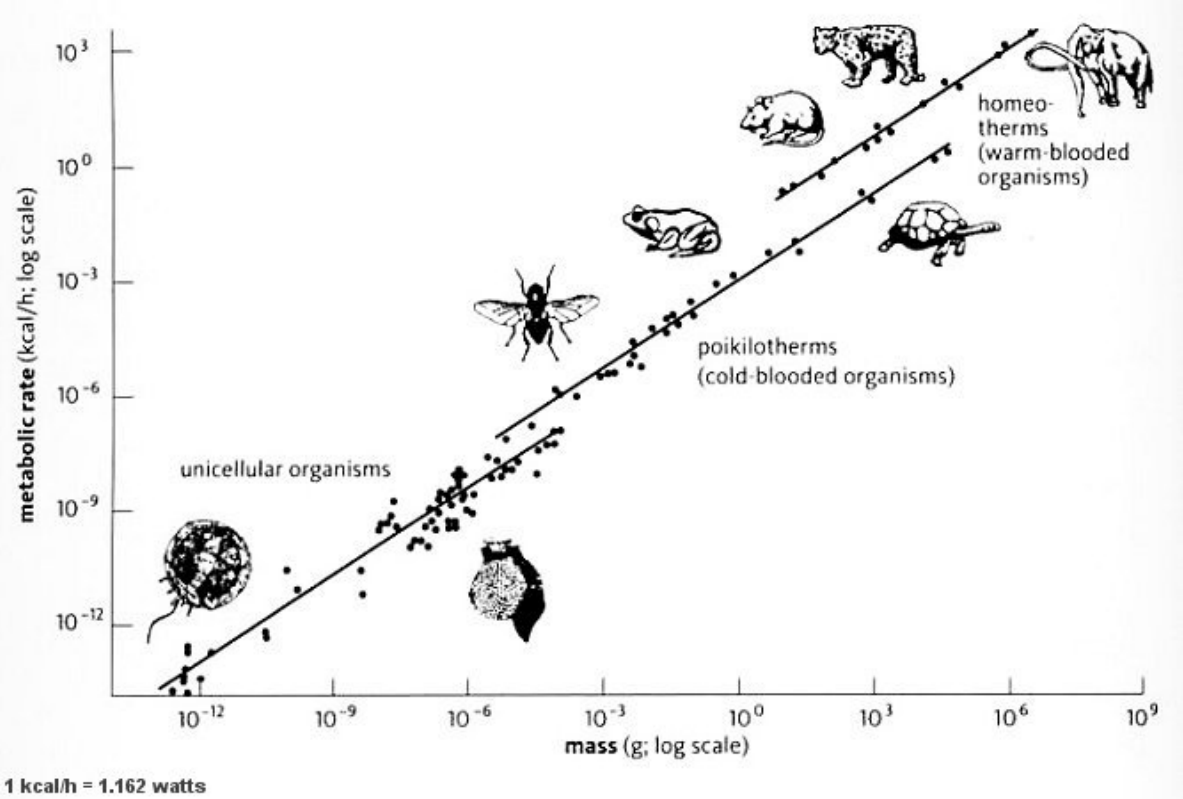
## *T. rex.*



http://www.english-online.at/science/dinosaurs/tyrannosaurus-rex.jpg

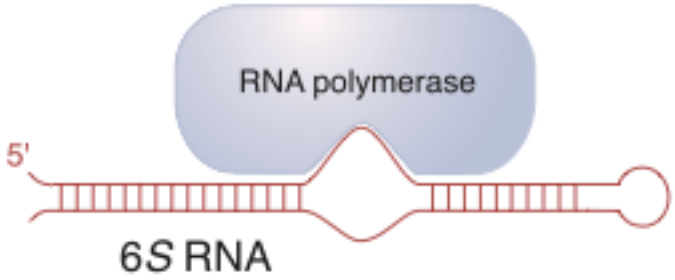
"How *Tyrannosaurus* used its tiny front legs is a scientific puzzle; they were too short even to reach the mouth. They may have been used to help the animal rise from a lying position". Boston's Museum of Science.

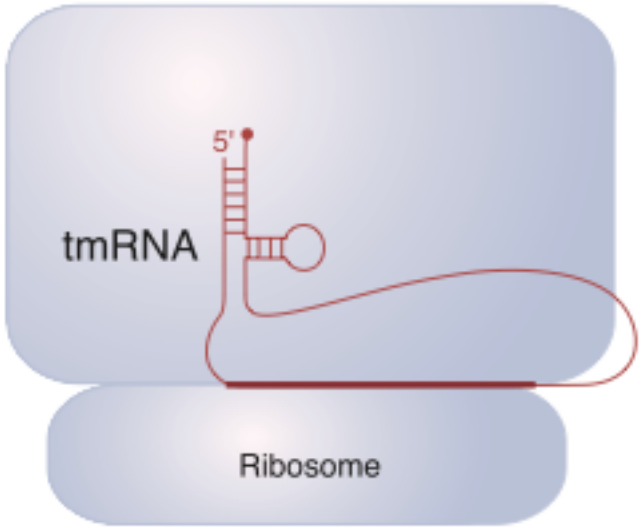
# *Evolution and allometric scaling.*

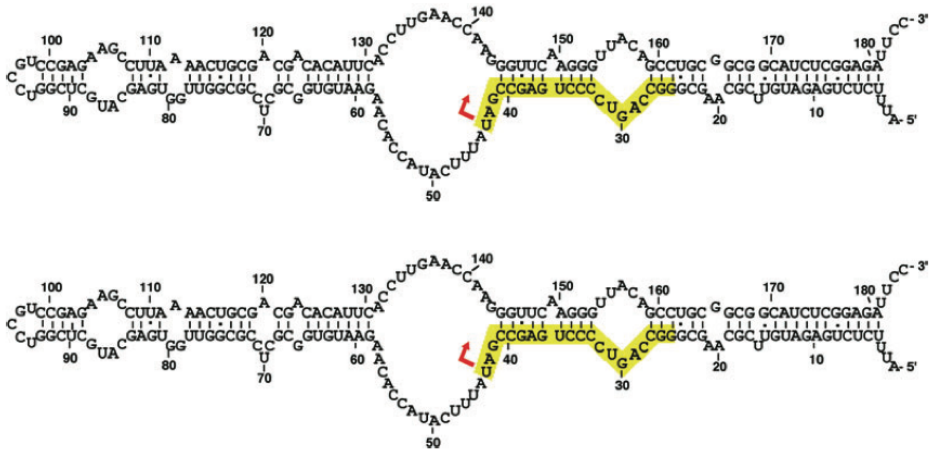



http://www.patternsinnature.org/Book/Scaling.html

# *The function of S6 genes*



Storz (2002)

Wassarmann (2007)

# Adaptation, Non-adaptive processes and Molecular alphabets

Evandro Ferrada
*Santa Fe Institute*

## *The menu*

- History of adaptationism
- Contemporary adaptation
- Requirements for the study of adaptation. Historical & Non-historical adaptation.
- Adaptation and genetic architecture
- Molecular alphabets.

## *The oldest ideas. Causation & Purpose.*

Aristotle
( 384 – 322 BC )

- Material
- Formal

- Efficient
- Final

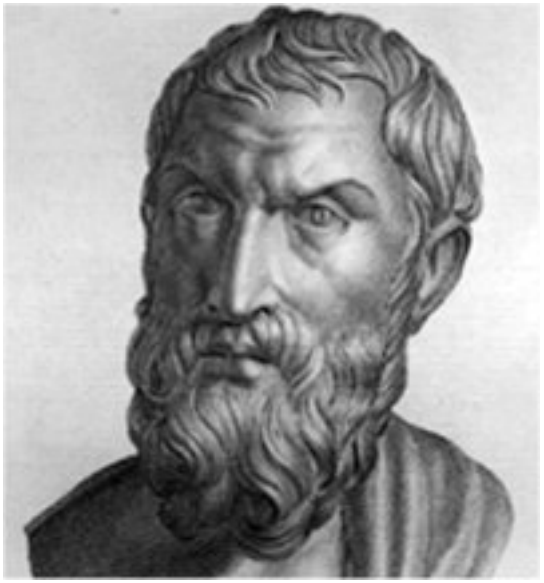
*Final cause* comes into existence only after the object which is the purported effect of that cause.

PAST ← PRESENT

*External Teleology* → Intelligent mind. (Plato, British natural theology).

*Internal Teleology* → Cosmos goalward. (Aristotle, Lamarck, H. Spencer).

## *The oldest ideas. Causation & Purpose.*



Titus Lucretius Carus
( c. 99 BC – c. 55 BC)

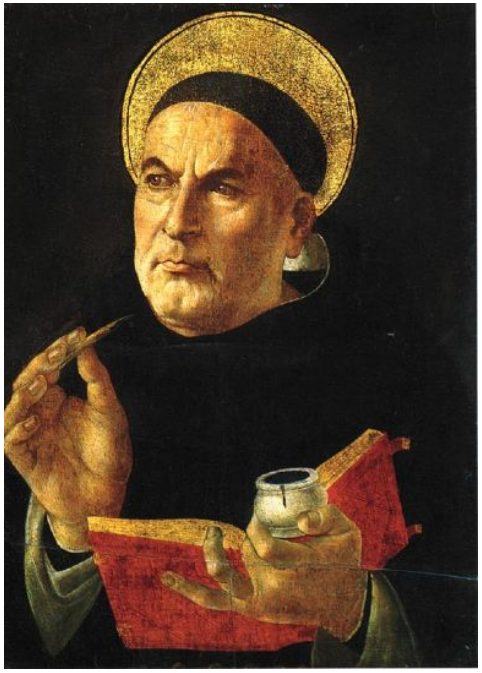
- Epicureism : against final causation.
- Epicureism accepted final causation for objects. But final causes and purposes could never explain the existence of natural objects.

## *Order and perfection in the living world*

Claudius Galenus
(AD 129 – c. 200/c. 216)

*"Nature does everything for some purpose, so that there is nothing ineffective or superfluous, or capable of being better disposed"*

*"Therefore some intelligent being exists by whom all natural things are directed to their end…"*

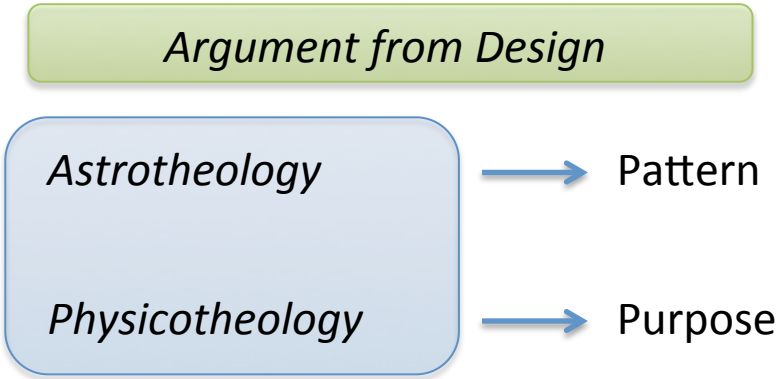


Thomas Aquinas
(1225 - 1274)

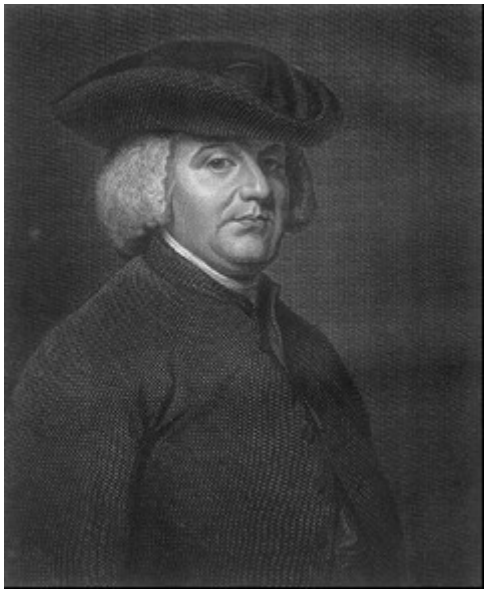
## *Celestial motions and the "Argument from Design"*

Sir Isaac Newton
(1642 - 1727)

- Newton's motion laws provided a distinction between the astronomical and organic bases for the inference of intelligent creation.
- Newton believed that the facts of astrophysics gave evidence for divine contrivance of the universe.



## *The birth of biological adaptationism*



William Paley
(1743 - 1805)

William Whewell
(1794 - 1866)

1802: Natural Theology.
1833: The Bridgewater Treatise.

## *Creation & Evolution. Teleology & Anti-teleology.*

Georges Cuvier
(1769 - 1832)

Teleologists → Function → Adaptationists → *Conditions for existence* → Purpose

Anti-teleologists → Form → Structuralists → *Unity of type* → Pattern

E.G. Saint-Hilaire
(1772- 1844)

*Idealistic morphology*
*Trascendental anatomy*
*Higher anatomy.*

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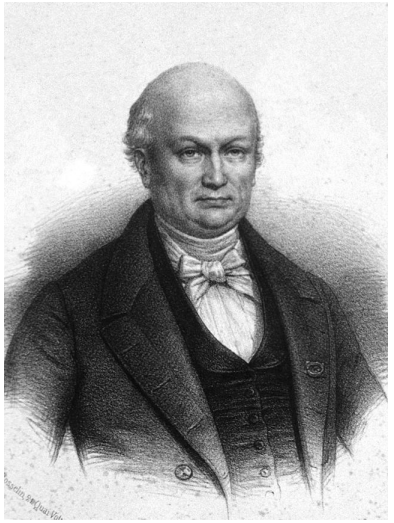


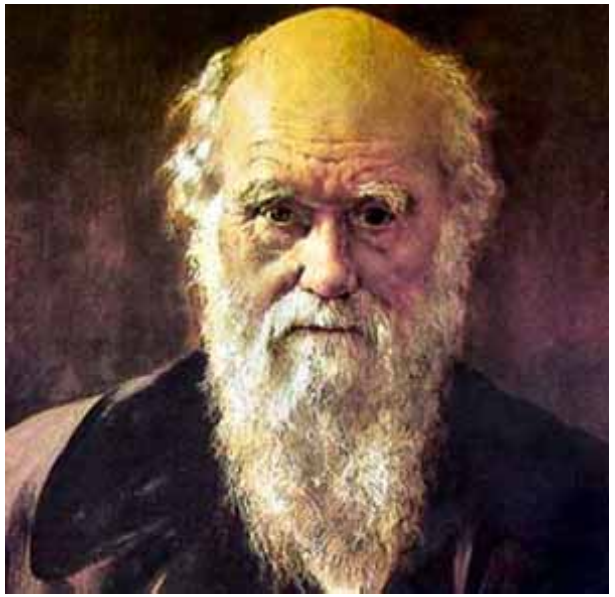
E.G. Saint-Hilaire
(1772- 1844)

*Idealistic morphology*
*Trascendental anatomy*
*Higher anatomy.*

*For the **adaptationist**, structure simply followed functional need. For the **structuralist**, function was merely the 'putting to use' of the products of structural laws.*

## *Adaptation in the Natural Selection context*

- Natural selection was the first and only fully naturalistic explanation of biological adaptation.



Charles Darwin
(1809 - 1882)

## *Adaptation in the Natural Selection context*

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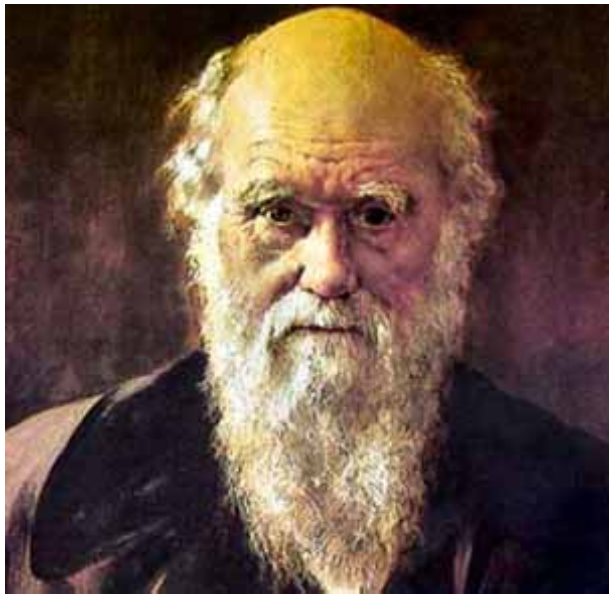
- Darwin connected the well-known phenomena of structuralist biology with his hypothesis of descent with modification.

    - Darwin adhered to the structuralists in that structure precedes function in functionally distinct homologs. Structure came first.



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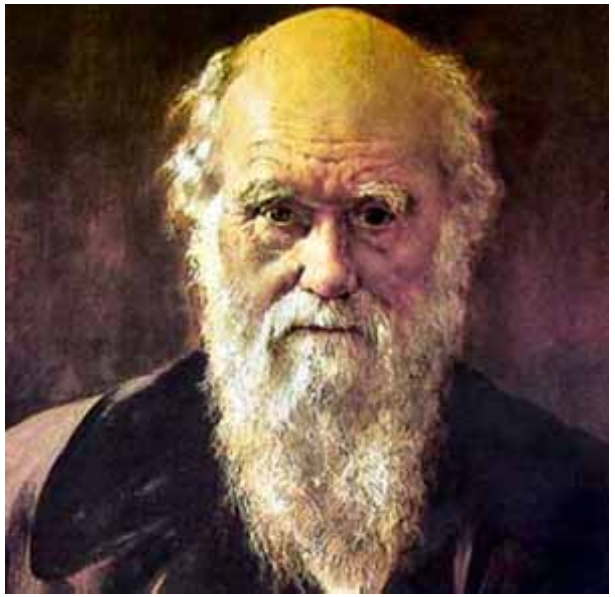

Charles Darwin
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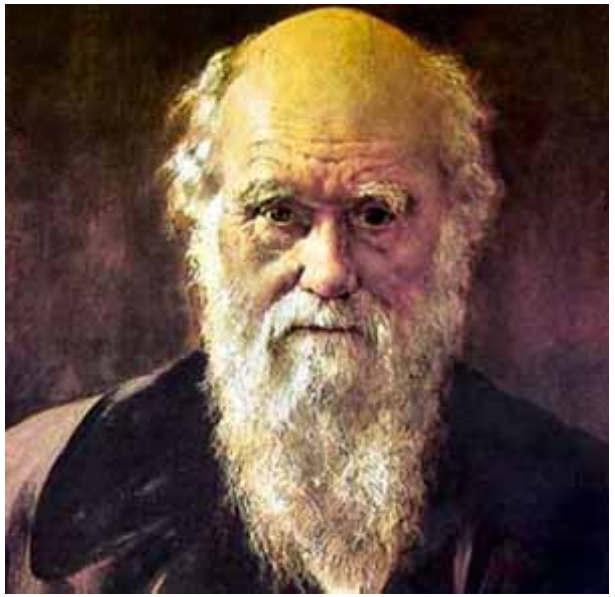
*"The condition of every animal is partly due to direct adaptation and partly to hereditary taint."*

(Darwin, Notebook B. 1837)

## *Pririority of function over structure*

*"Hence, in fact, the law of the Conditions of Existence is the higher law, as it includes, through the inheritance of former adaptations, that of the Unity of Type".*

Origins (Chapter 4).



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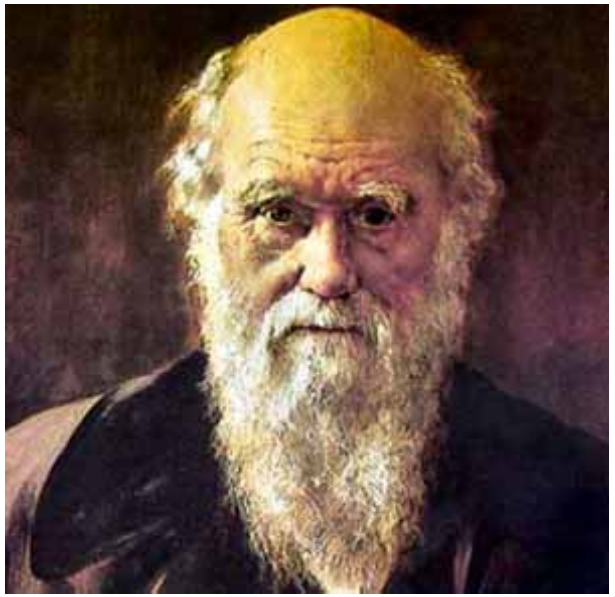

Charles Darwin
(1809 - 1882)

1) The origins gave a unified account of both adaptationist and structuralist biology.

2) Darwin considered adaptivity to be a *higher law,* that preceedes structure.

## *Challenges to the Origins view of adpatation. Drift and Development.*

Gould & Lewontin (1979)

# The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme

By S. J. Gould and R. C. Lewontin

*Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts* 02138, *U.S.A.*

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Gould & Lewontin (1979)

## *Contemporary adaptation*

- “apt-us” : fitted, suited, appropriate.
- “ap-ere” : to fasten, attach.

- Adaptation refers to a process and to the product of this process.
- Adaptation is a relational process. The fitting of one thing to another.

An *adaptation* is a modified part of an organism which performs a biological function for the organism and thus, contributes to the organism’s state of adaptation.

Historical

A current trait is an adaptation for a current use just in case it arose by natural selection for that use. *Adaptation*. (*Aptation).*

Non-historical

A current trait is an adaptation just in case it contributes to current fitness. *Exaptation*. (*Aptation).*

## *Contemporary adaptation*

Historical

A current trait is an adaptation for a current use just in case it arose by natural selection for that use. *Adaptation*. (*Aptation).*

Non-historical

A current trait is an adaptation just in case it contributes to current fitness. *Exaptation*. (*Aptation).*

When the causes are discovered to be natural selection, the traits would be pronounced adaptations.

## *The study of adaptation.*

| | |
|---|---|
| Historical | Purpose. Phylogeny. |
| Non-historical | Pattern. Genetic architecture. |

## *The study of adaptation.*

| | |
|---|---|
| Historical | Purpose. Phylogeny. |
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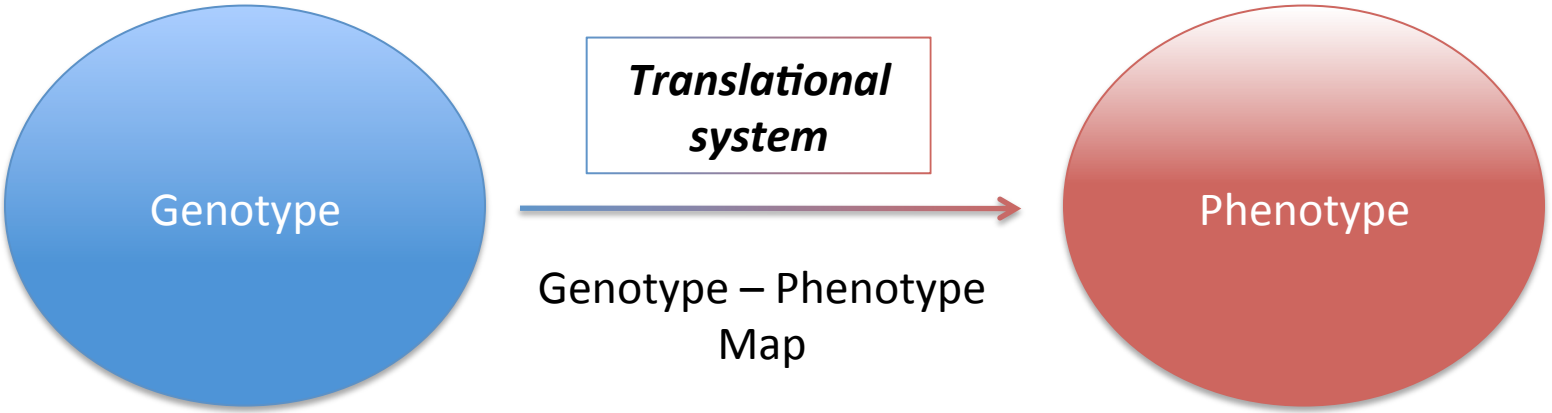
*"We do not need to understand the genetic architecture of traits to ascertain whether those traits are adaptations."*

G.J. Vermeij.

## *The study of adaptation and genetic architecture.*

Historical — Purpose. Phylogeny.

Non-historical — Pattern. Genetic architecture.



**Phenotype**

**Genotype**

**Structure**

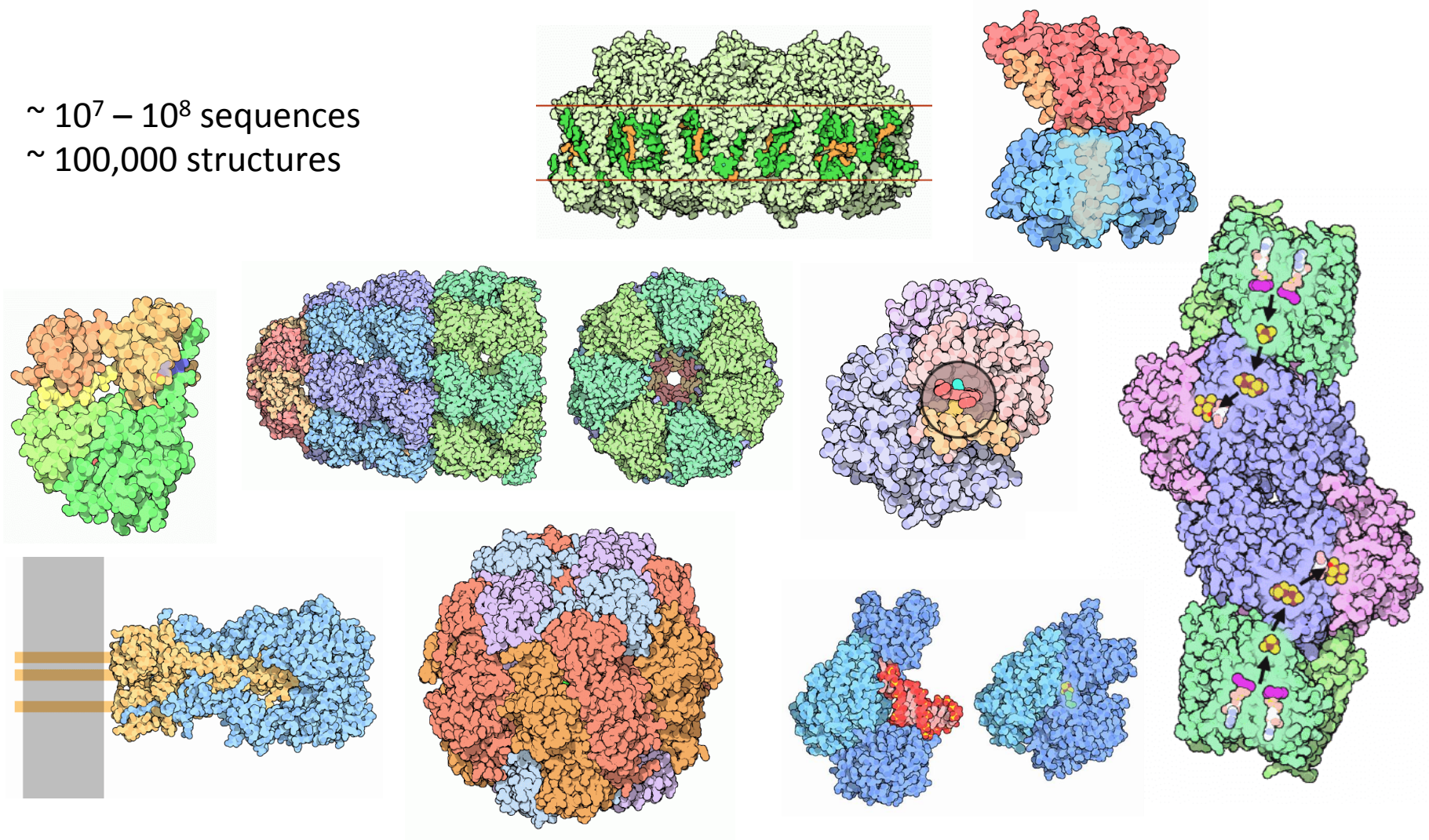
*Folding problem*

**Sequence**

```
MPLLLLLLLLPSPLHPHPICEVSKVASHLEVNCDKRNLTALPPDLPKDTTILHLSENLLYTFSLATLM
PYTRLTQLNLDRCELTKLQVDGTLPVLGTLDLSHNQLQSLPLLGQTLPALTVLDVSFNRLTSLPLGAL
RGLGELQELYLKGNELKTLPPGLLTPTPKLEKLSLANNNLTELPAGLLNGLENLDTLLLQENSLYTIP
```

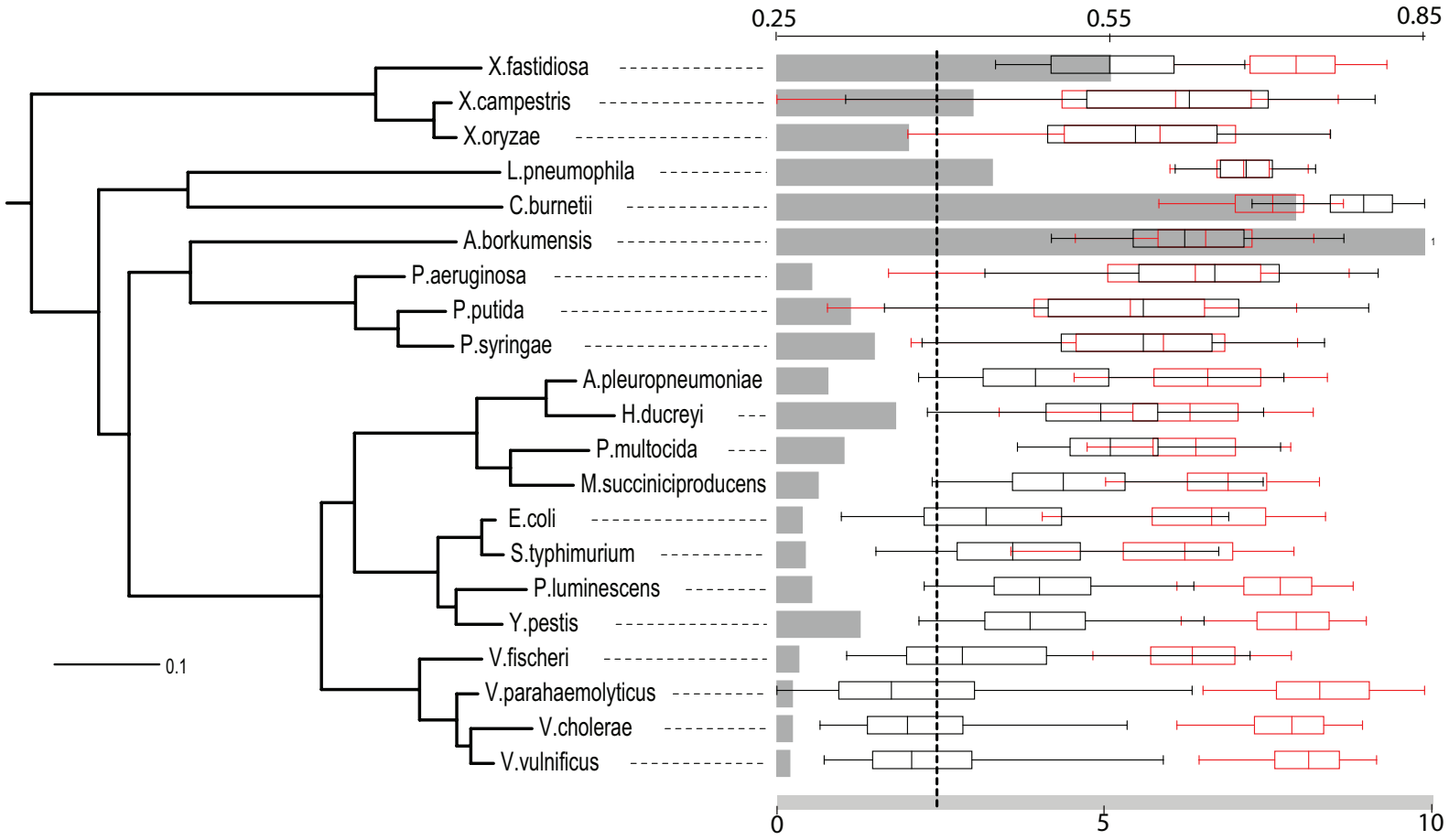
# *The diversity of protein structures & functions*

~ $10^7$ – $10^8$ sequences
~ 100,000 structures



*RSCB Protein Data Bank*

# *Historical: Phylogeny*



## *Non-historical: Genetic architecture*

## *Genotype space*

- J. Maynard-Smith (1970)

"Suppose now that we imagine all possible amino-acid sequences to be arranged in a 'protein space', so that two sequences are neighbors if one can be converted into another by a single amino-acid substitution."

## *Genotype space*

- J. Maynard-Smith (1970)

Metric space.

- Set of objects.
- Distance measure.

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Genotype space : $S(L, |\boldsymbol{A}|)$
Size : $|\boldsymbol{A}|^L$

- $|\boldsymbol{A}|$ : Monomer alphabet size
- L : Sequence length

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Genotype space : $S(L, |\boldsymbol{A}|)$
Size : $|\boldsymbol{A}|^L$

- $|\boldsymbol{A}|$ : Monomer alphabet size
- L : Sequence length

- Dimensionality
  $n = L\,(|\boldsymbol{A}|-1\,)$

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Sequence distance: $d(s_i,s_j)$

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*Metric space.*

- Set of objects.
- Distance measure.

*Genotype space.*

- All possible sequences.
- Sequence distance.

Sequence distance: $d(s_i, s_j)$

1. $s_1$: HPHPHP
2. $s_2$: HPPPHP
3. $s_3$: PHPHPH

$d\ (\ s_1, s_2\ ) = 1.$

$d\ (\ s_1, s_3\ ) = 6.$

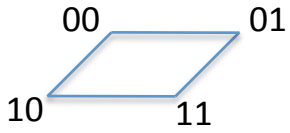
## *Hypercubes or n-cube*

$|A|=2$ , L=1

$S(1,2)$

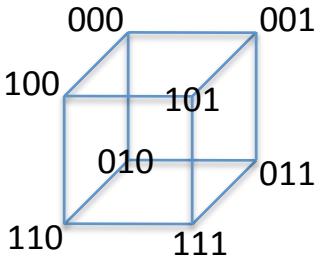

$|A|=2$ , L=2

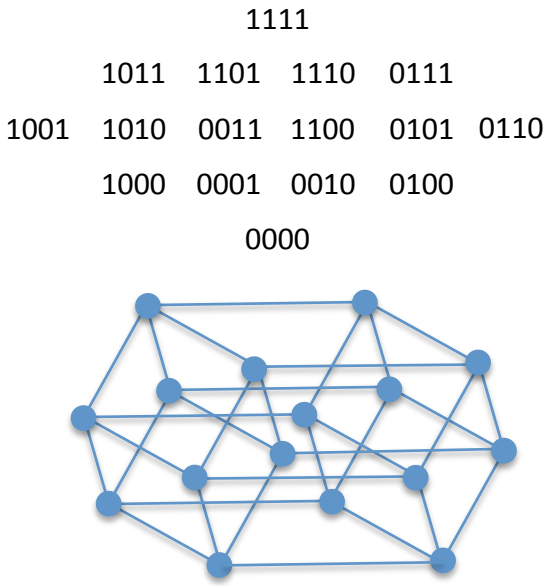
$S(2,2)$




$|A|=2$ , L=3

$S(3,2)$

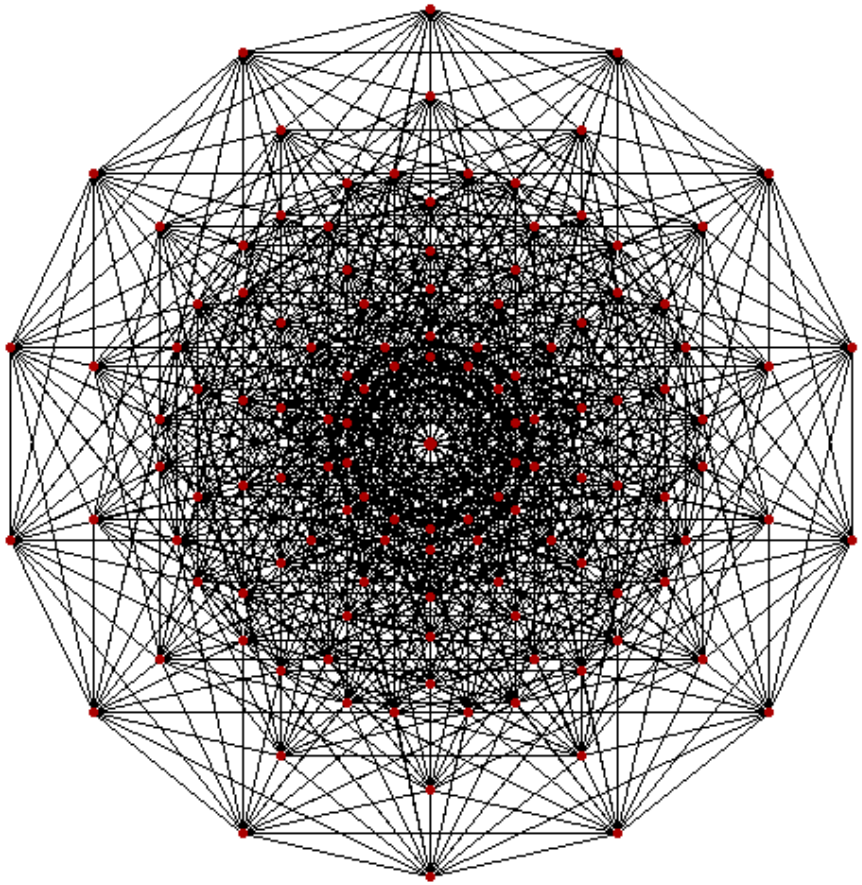



$|A|=2$ , L=4

$S(4,2)$

## *The Protein Sequence Space as a n-cube*

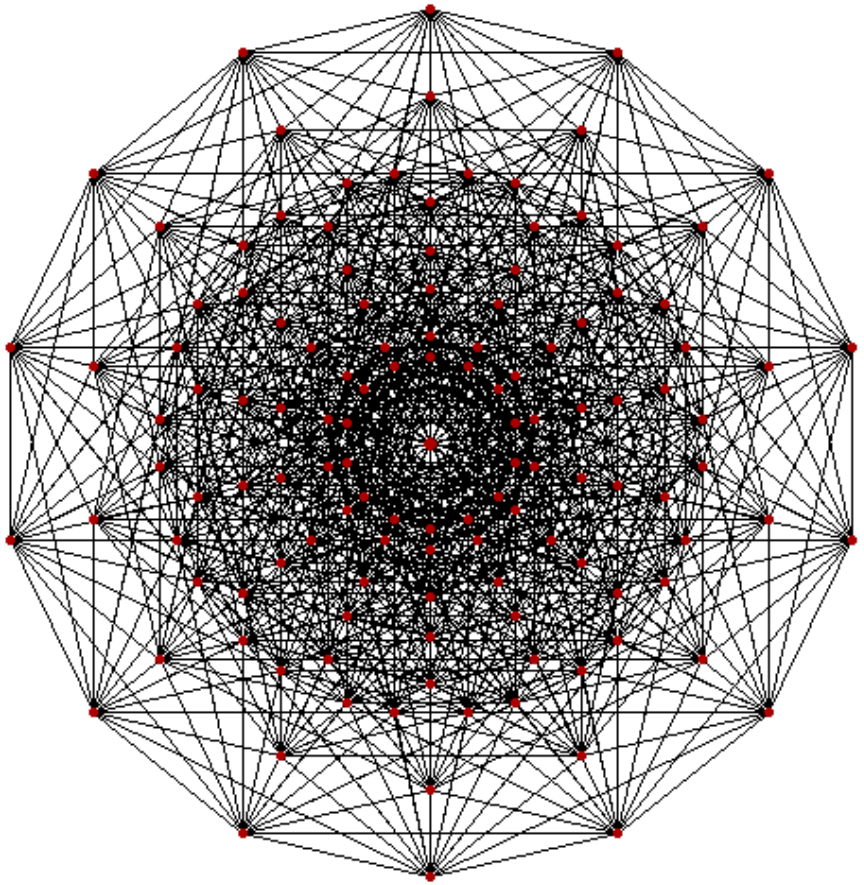


$Q_2^7$ 7-cube

www.sonic-arts.org/chalmers/

## *The Protein Sequence Space as a n-cube*

… a generalized hypercube: $Q^L_{|A|}$



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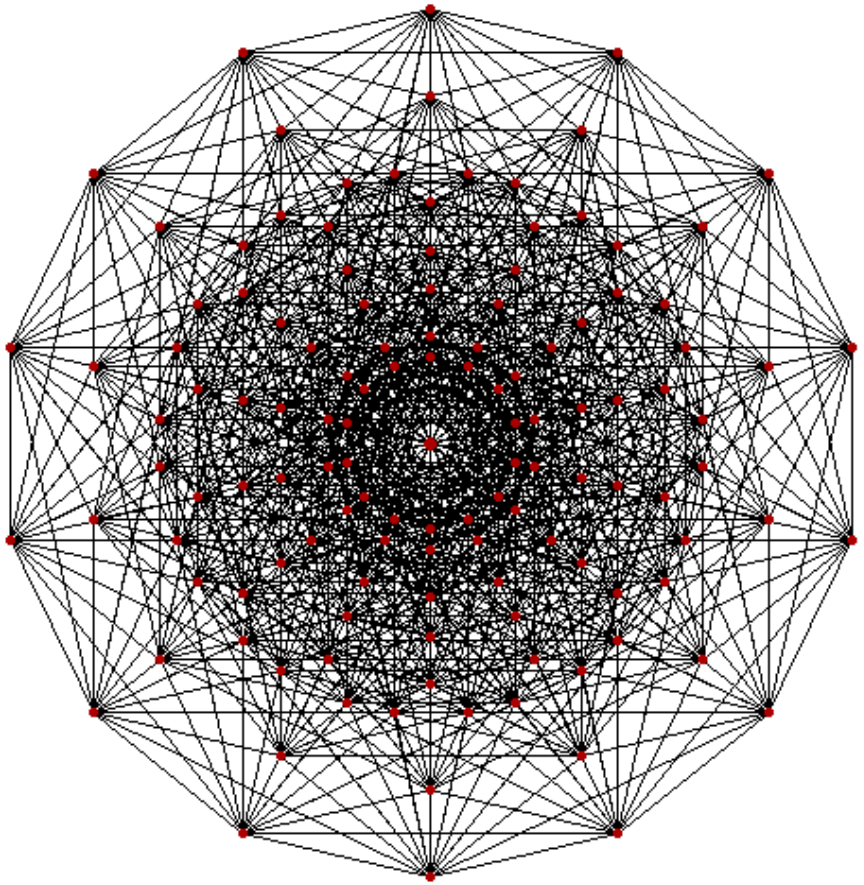
… a generalized hypercube: $Q^L_{|A|}$

Genotype space :

$S(L, |\boldsymbol{A}|) = Q^L_{|A|}$



$Q^7_2$ 7-cube

www.sonic-arts.org/chalmers/

## *Phenotypes are embedded into genotype space*

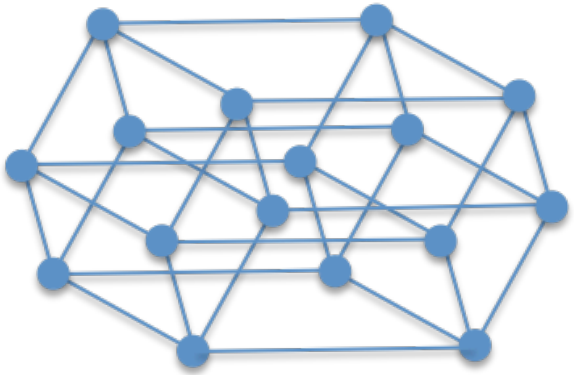
1111

1011 1101 1110 0111

1001 1010 0011 1100 0101 0110

1000 0001 0010 0100

0000



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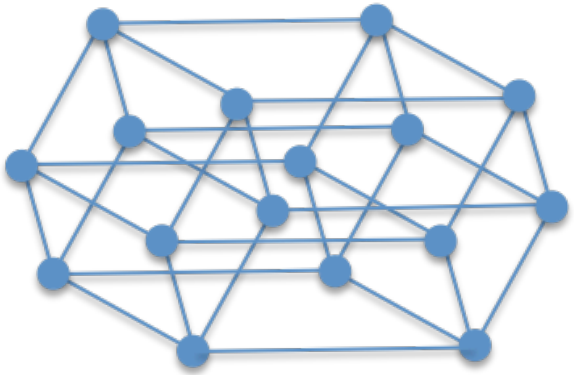
1011 1101 1110 0111

1001 1010 0011 1100 0101 0110

1000 0001 0010 0100

0000



1111

1011 1101 1110 0111

1001 1010 0011 1100 0101 0110

1000 0001 0010 0100

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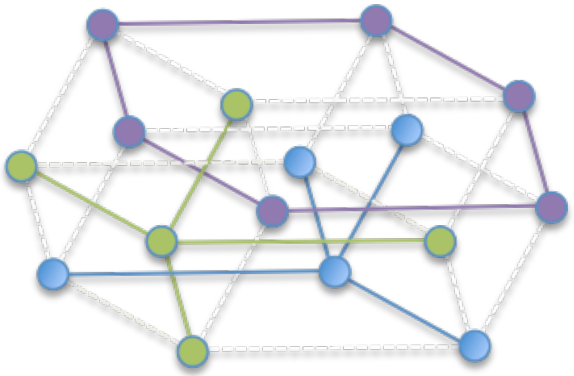

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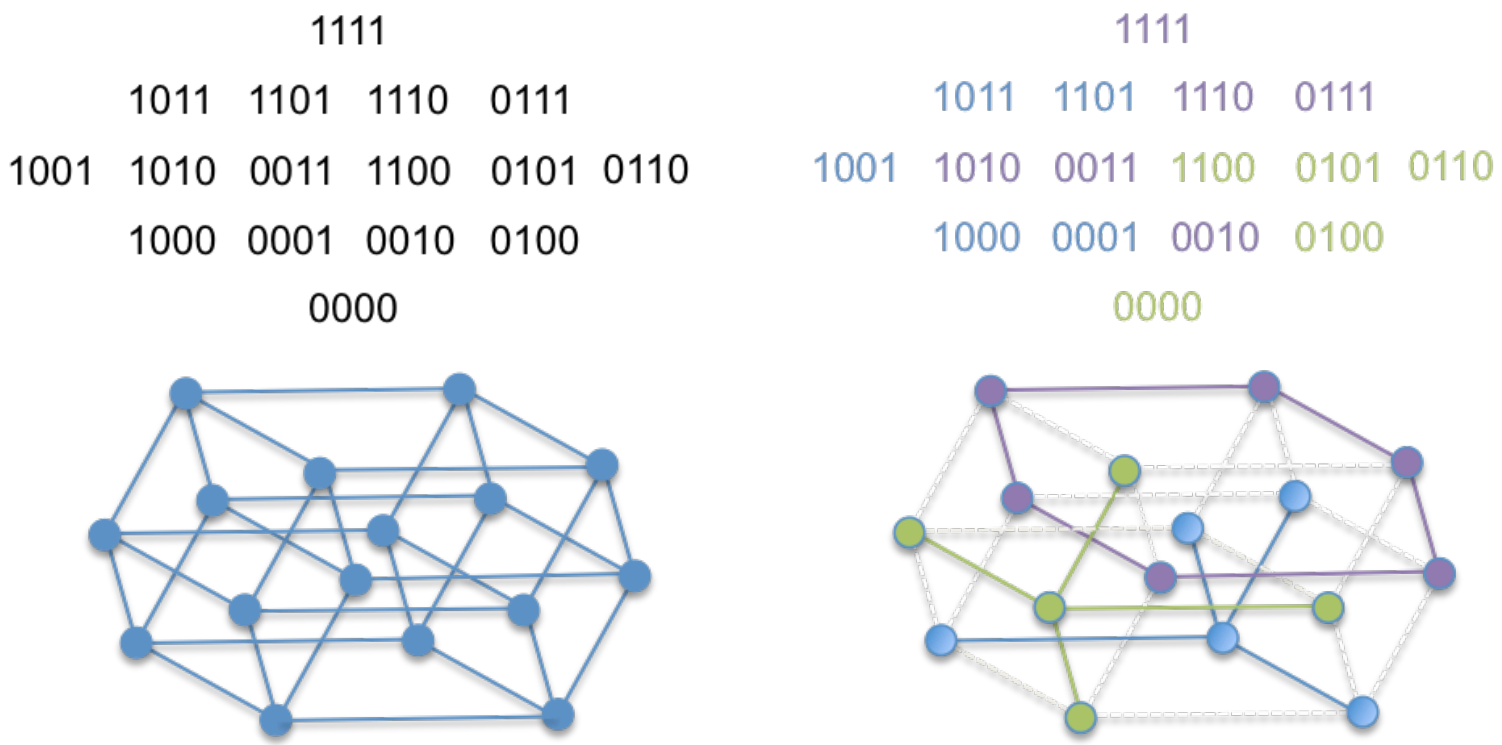
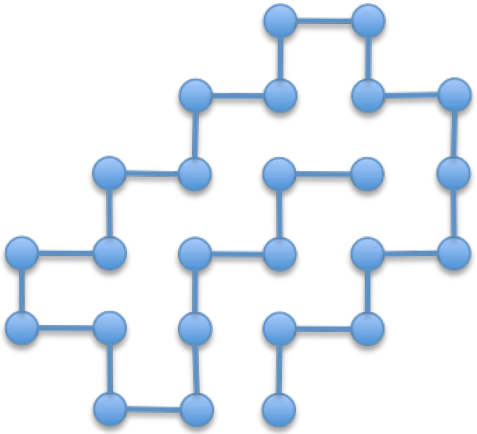
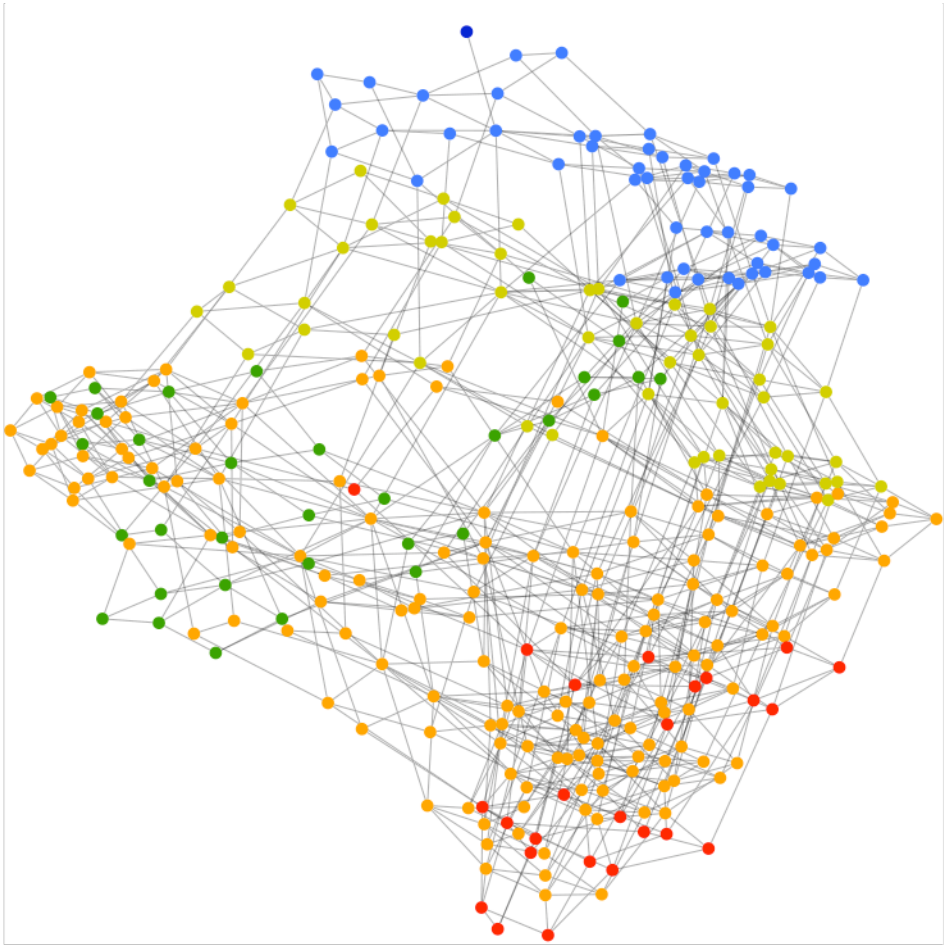


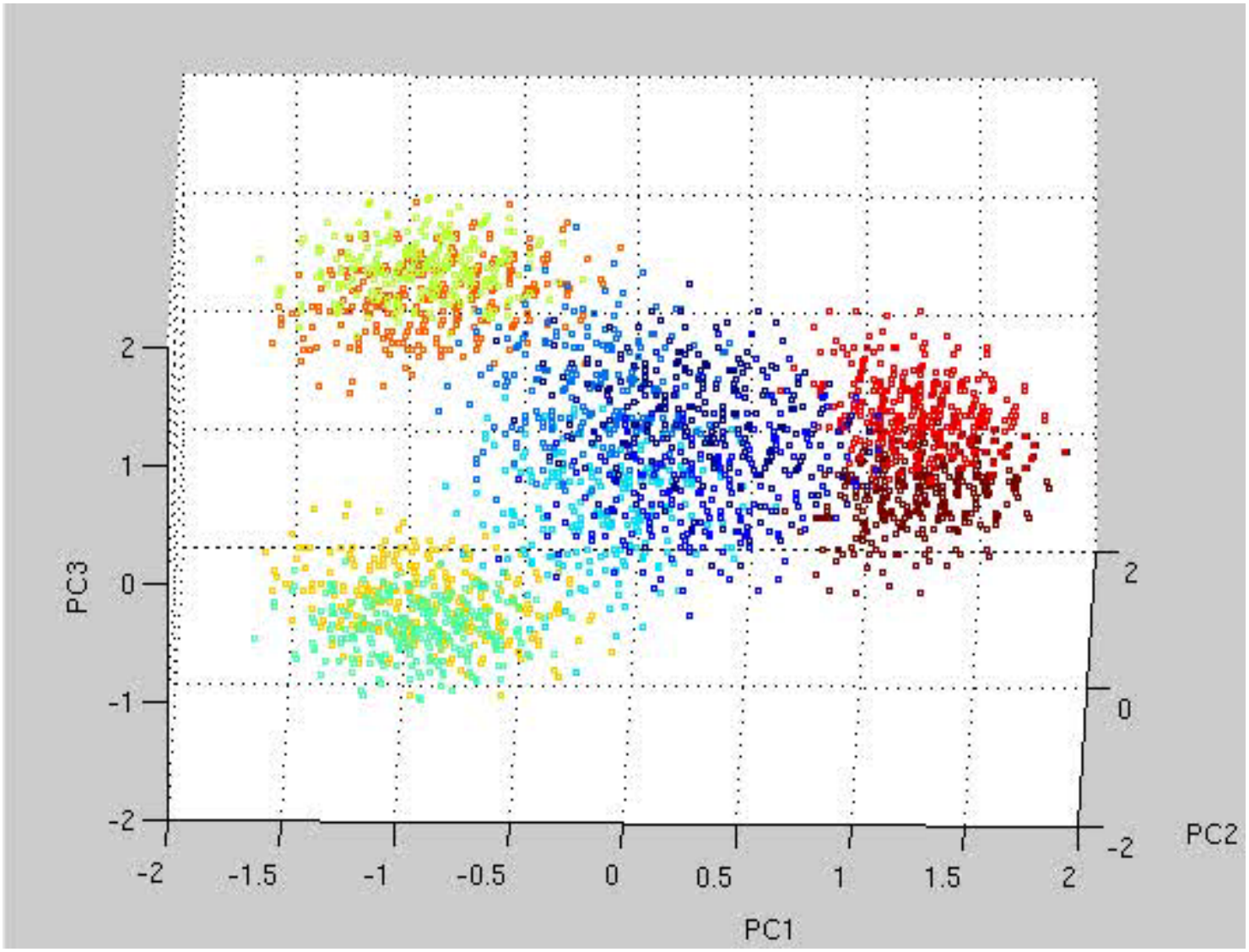

*Genotype (neutral) network:*

- Collection of **genotypes** that map to a single phenotype and can be connected by single point mutations.

# *Insights from simple exact models*






PC3
2
1
0
-1
-2
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
PC1
2
0
-2
PC2

## *Genotype space is a generalized hypercube*

Genotype space :

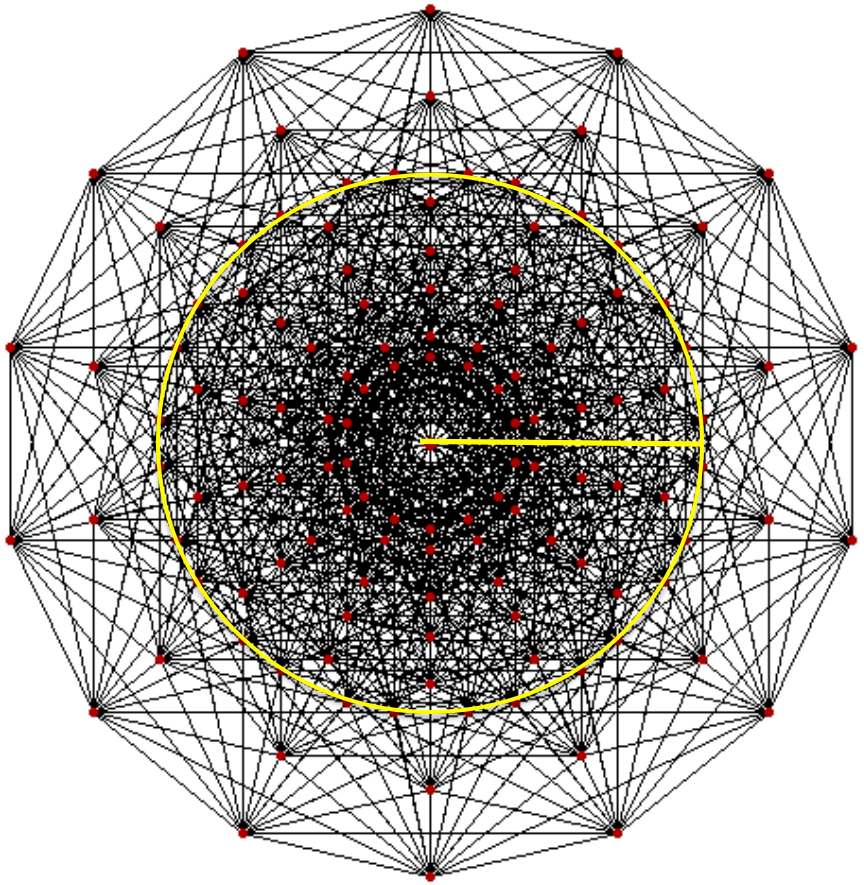
$S(L, |A|) = Q^L_{|A|}$

$S(L, 2)$

$$1 + L + \frac{L(L-1)}{2} + \ldots$$

$$V(k) = \sum_{i=0}^{i=k} \binom{L}{i} (|A| - 1)^i$$

$$A_B(k) = \binom{L}{k} (|A| - 1)^k$$

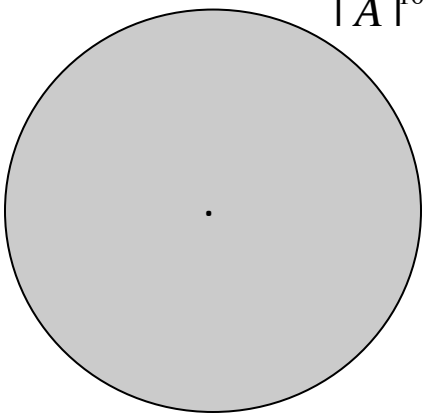


$Q^L_2$

www.sonic-arts.org/chalmers/

## *Genotype space is a generalized hypercube*

$$|A|^{100} = V_B(100)$$



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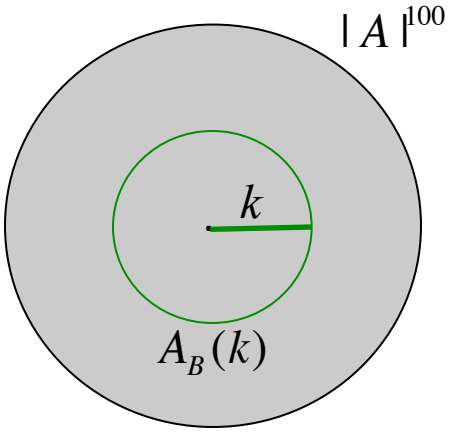
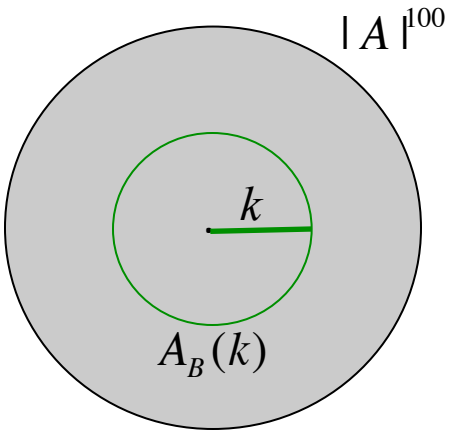
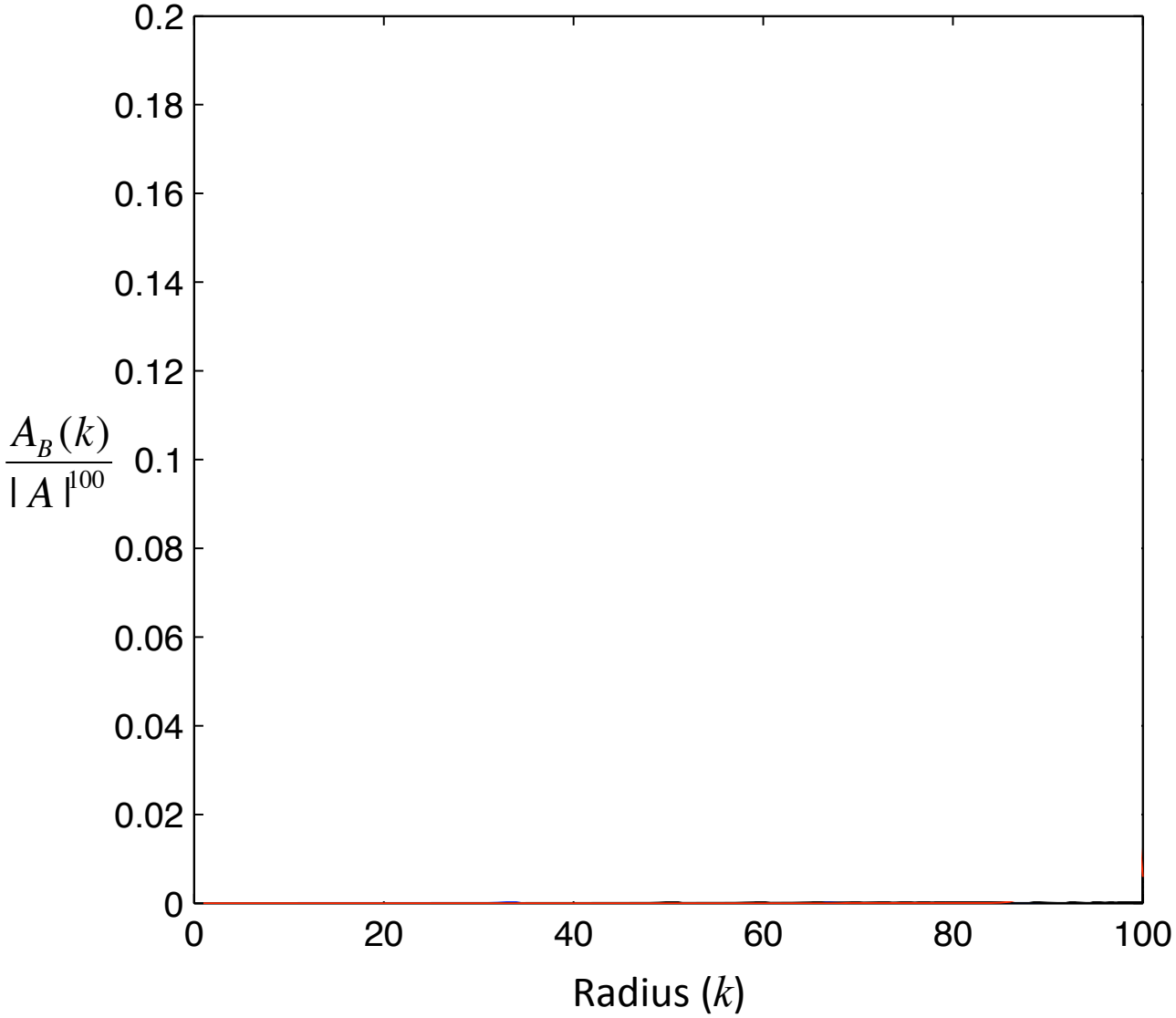
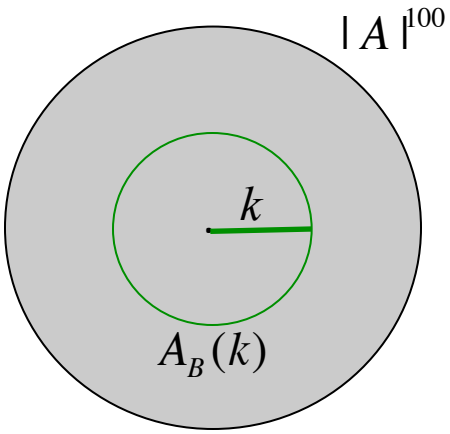


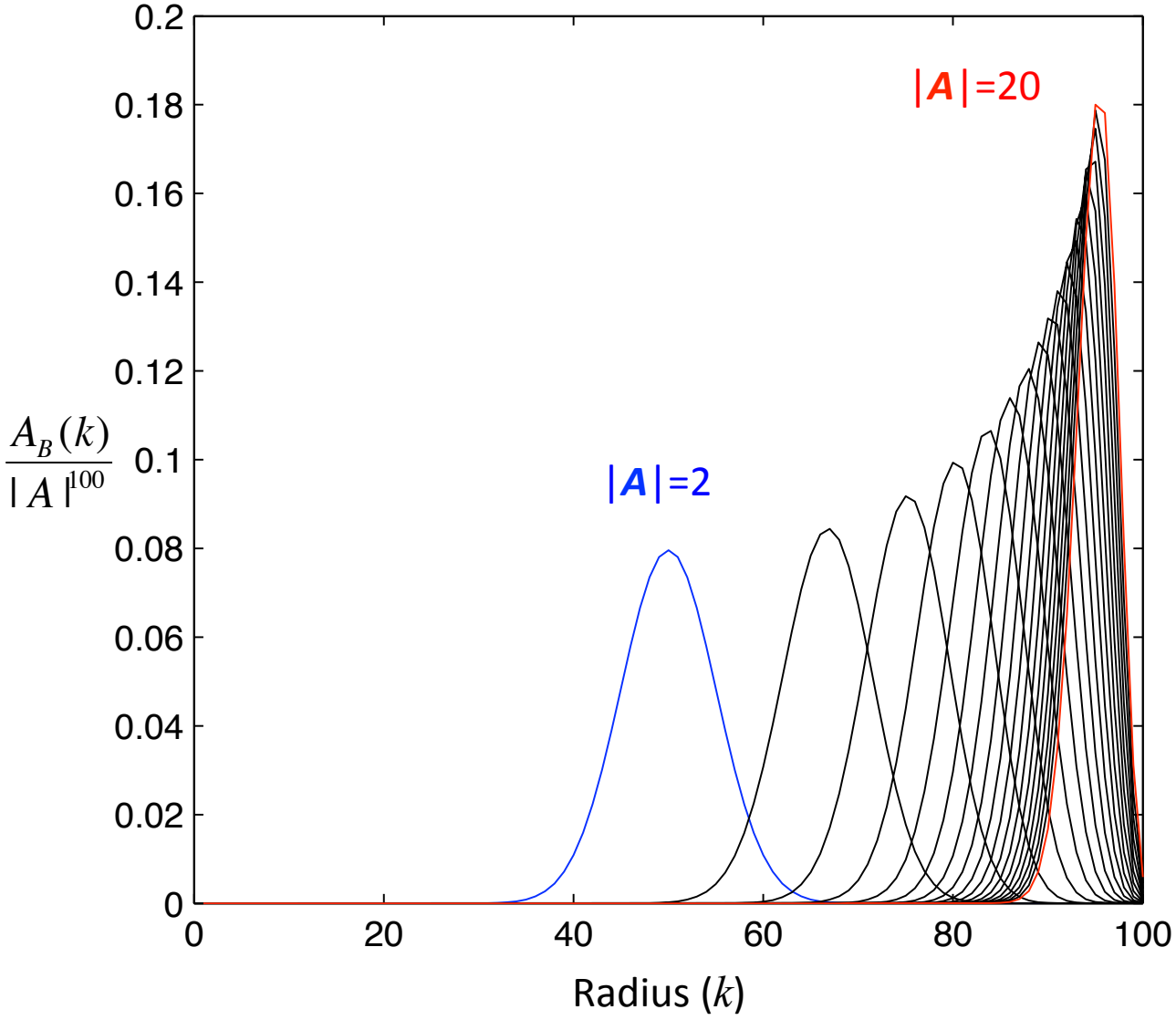
## *Genotype space is a generalized hypercube*



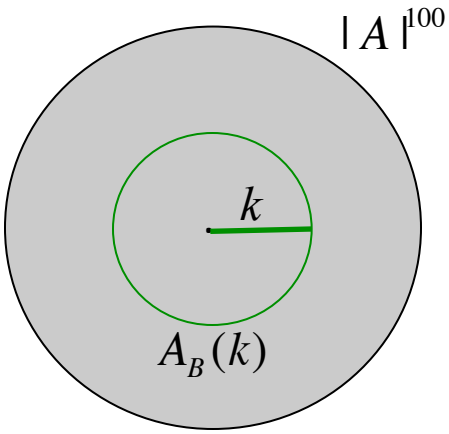



## *Genotype space is a generalized hypercube*



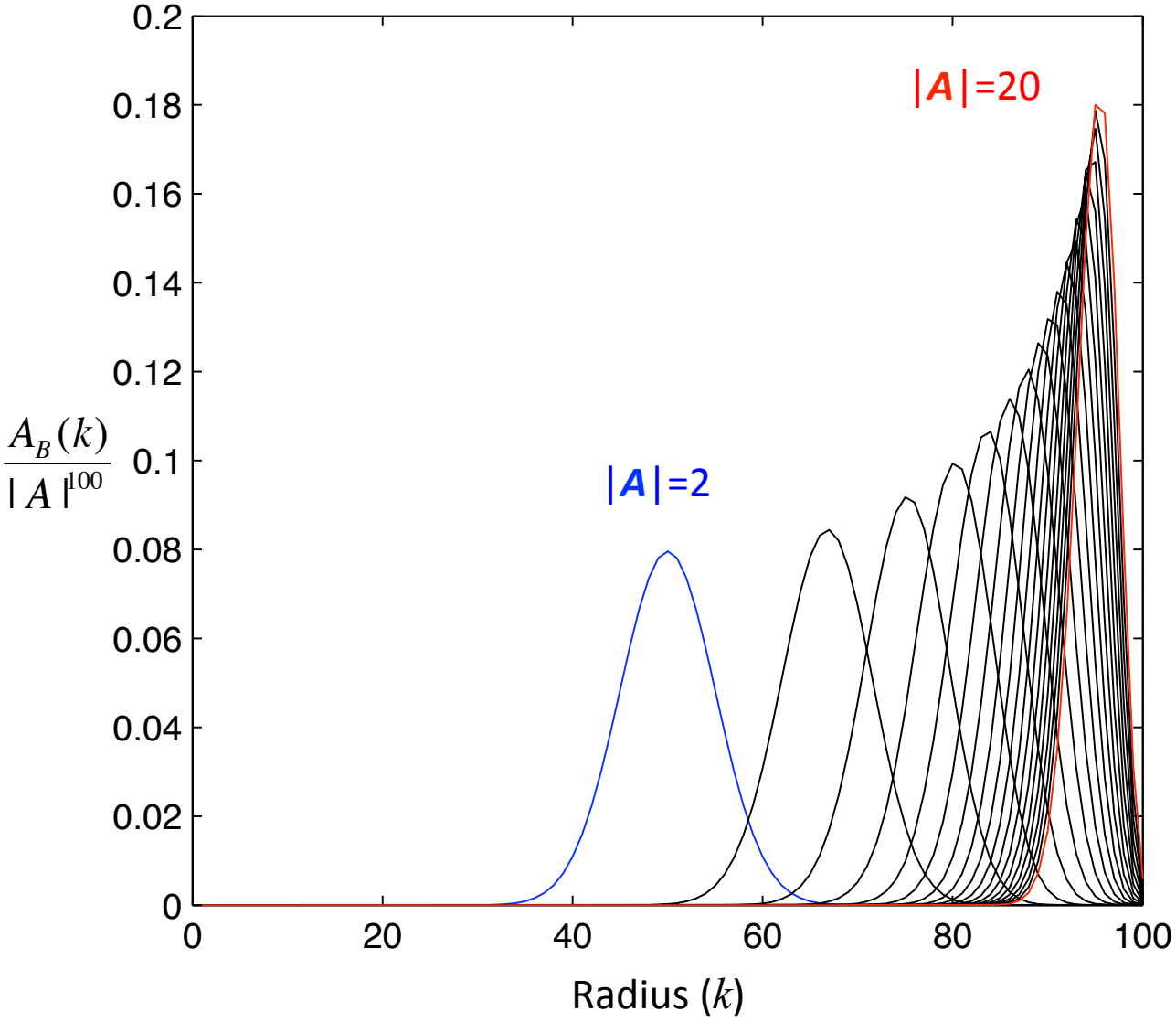



## *Genotype space is a generalized hypercube*

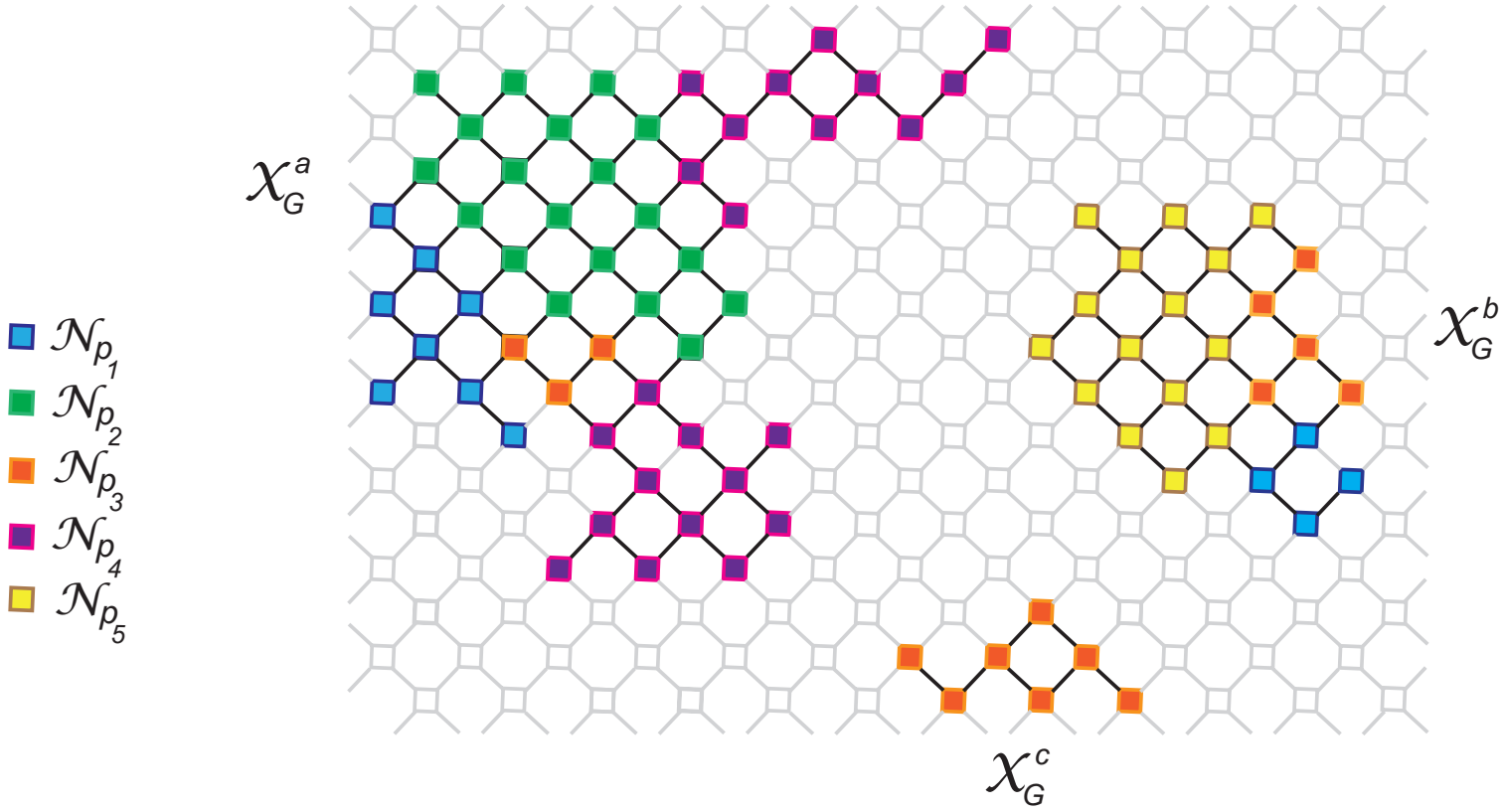



$$k \sim 1 - \frac{1}{|A|}$$

*Random threshold of sequence divergence*

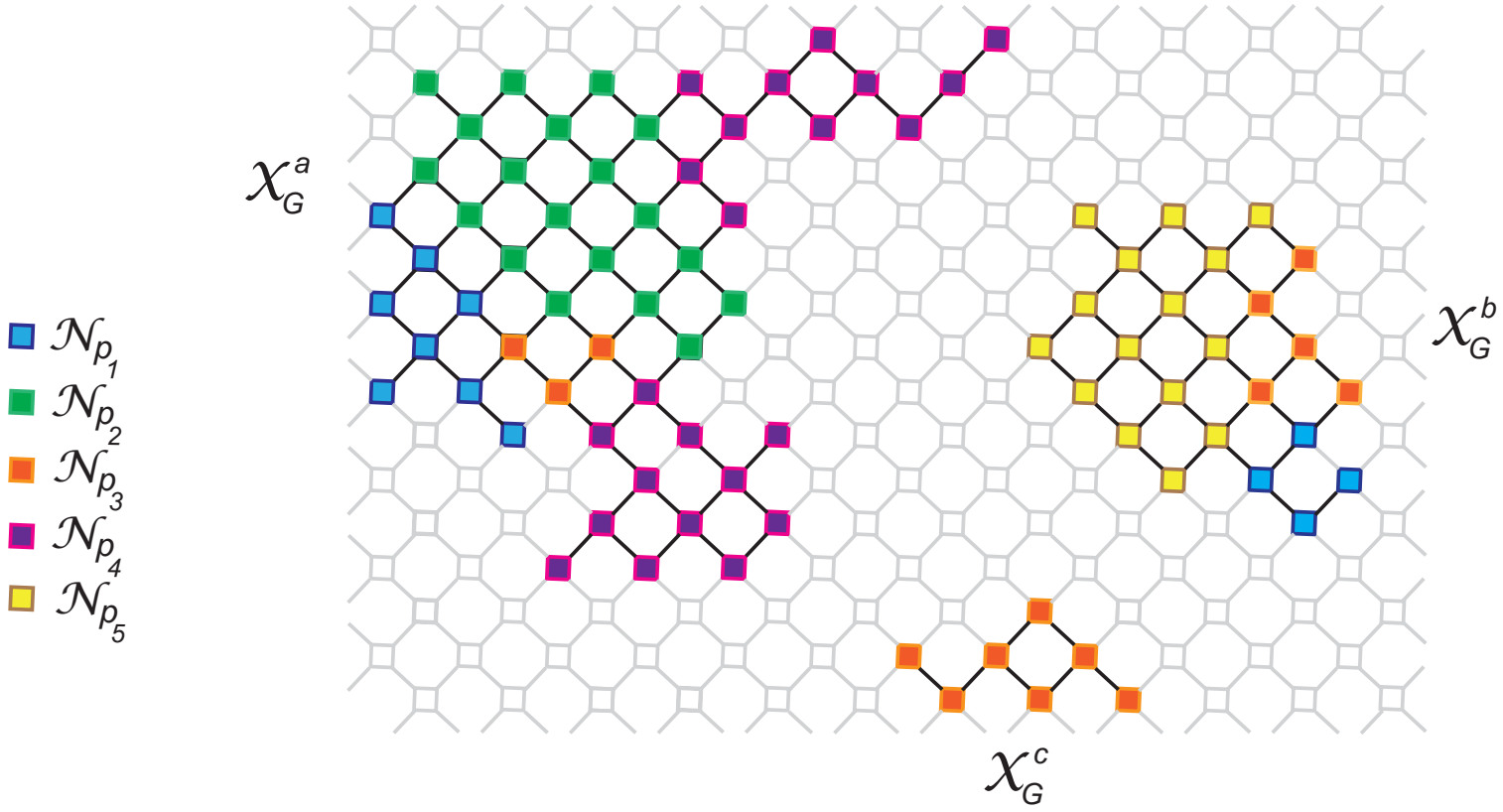


## *Networks and connected components in genotype space.*



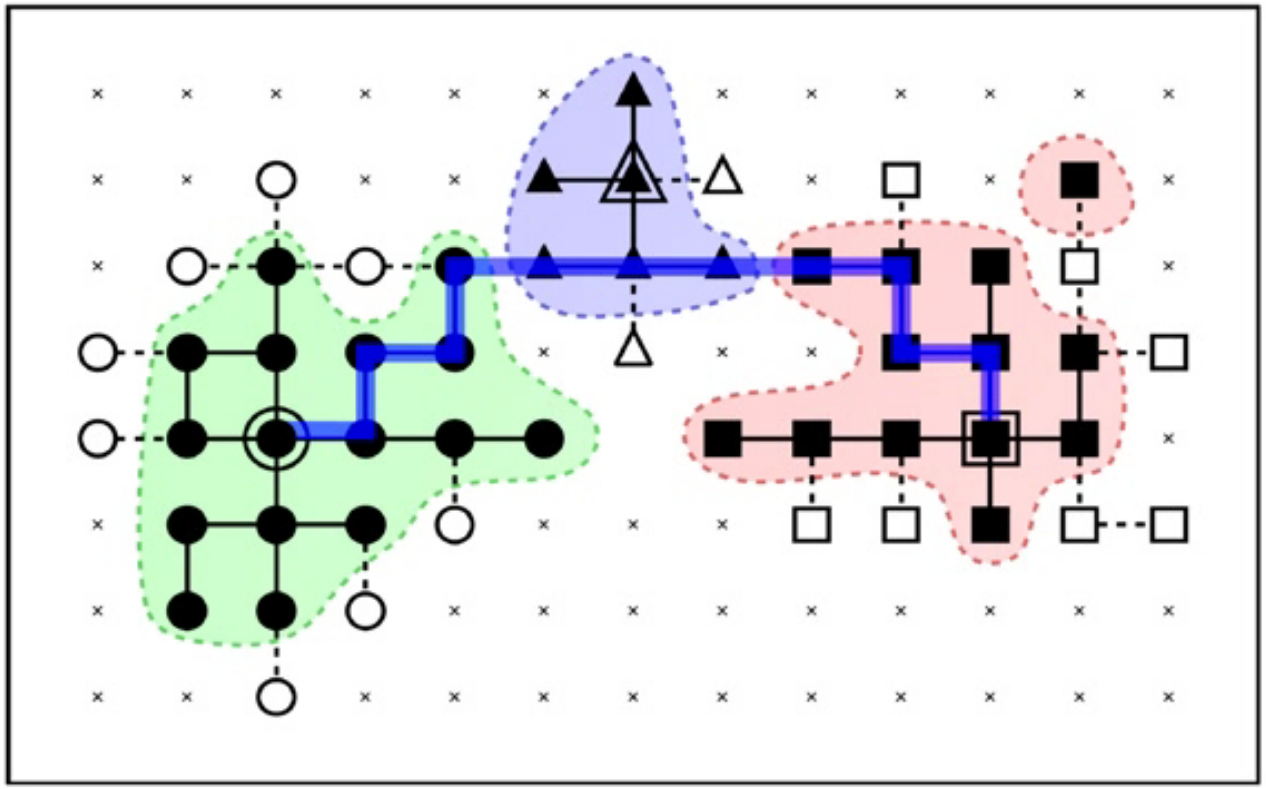

- Genotype component: $\boldsymbol{X}_G$
- Neutral set : $\boldsymbol{N}_P$
- Neutral network : $\boldsymbol{Y}_P$

## *Networks and connected components in genotype space.*



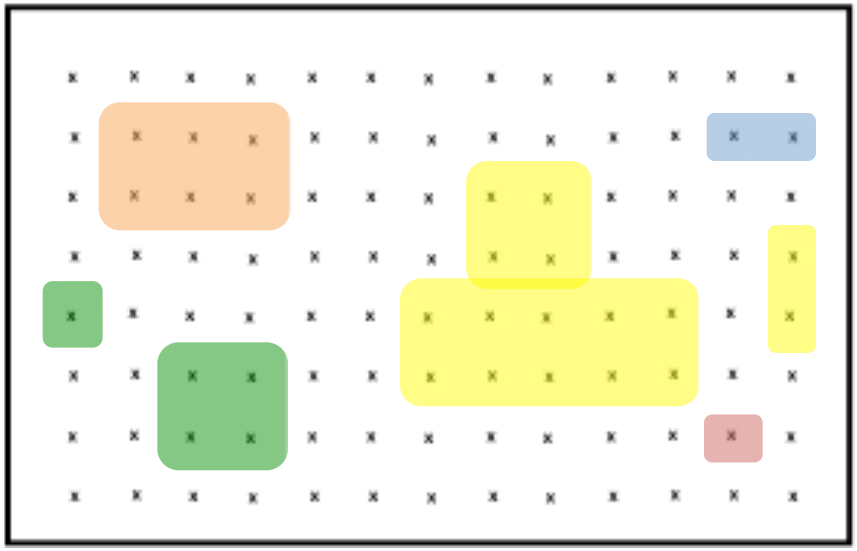

- Genotype component: $\boldsymbol{X}_G$
- Neutral set : $\boldsymbol{N}_P$
- Neutral network : $\boldsymbol{Y}_P$

- Designability
- Neutrality

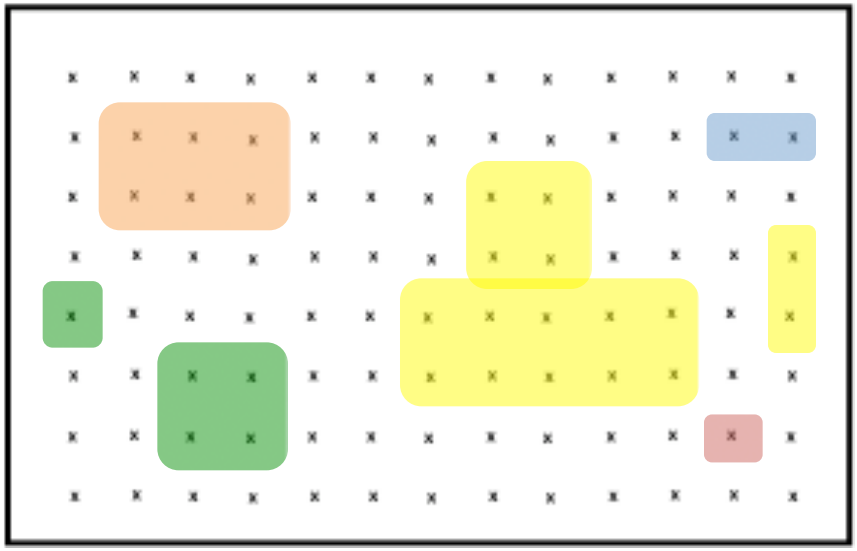


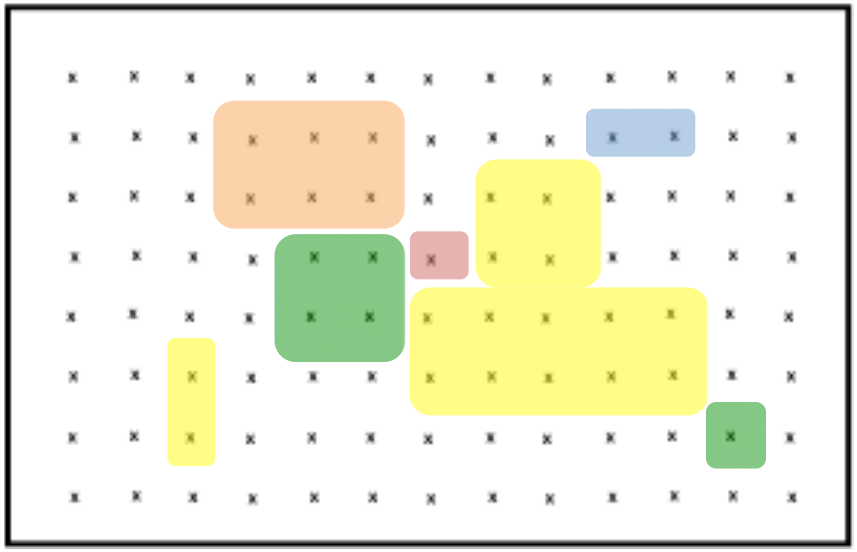
*HFSP J. 1:79 (2007).*

# *Robustness and evolvability as properties of the GP map*



# *Robustness and evolvability as properties of the GP map*





## *Conclusions & Summary*

- Adaptation is at the core of the old *pattern & purpose* debate. And therefore at the center of an explanation for the origins.
- At the XIX century, the main two ideas canalized into the teleology & anti-teleology debate.
- Darwin solved this debate by providing a theory that explains the origins of adaptations.
- Contemporary study of adaptation encompasses a historical and a non-historical component.

## *The study of adaptation.*

| | |
|---|---|
| Historical | Purpose. Phylogeny. |
| Non-historical | Pattern. Genetic architecture. |

## *The study of adaptation.*

| | |
|---|---|
| Historical | Purpose. Phylogeny. |
| Ontogenetic | Development. |
| Non-historical | Pattern. Genetic architecture. |

## *Conclusions & Summary*

- Historicism can be address comparatively by the comparison of extant species and their phylogeny.
- Non-historicism, or the study of pattern, centers on structural constraints, coarse graining and self-organization.
- Ontogenetic adaptation encompasses both, historic and non-historic approaches, and regards developmental constraints, lamarckian evolutionary processes and adaptation at short-time scales.

And yet it is hard to believe that anything
in nature could stand revealed as solid matter.
The lightning of heaven goes through the walls of houses,
like shouts and speech; iron glows white in fire;
red-hot rocks are shattered by savage steam;
hard gold is softened and melted down by heat;
chilly brass, defeated by heat, turns liquid;
heat seeps through silver, so does piercing cold;
by custom raising the cup, we feel them both
as water is poured in, drop by drop, above.

*De Rerum Naturae. Book I,.*