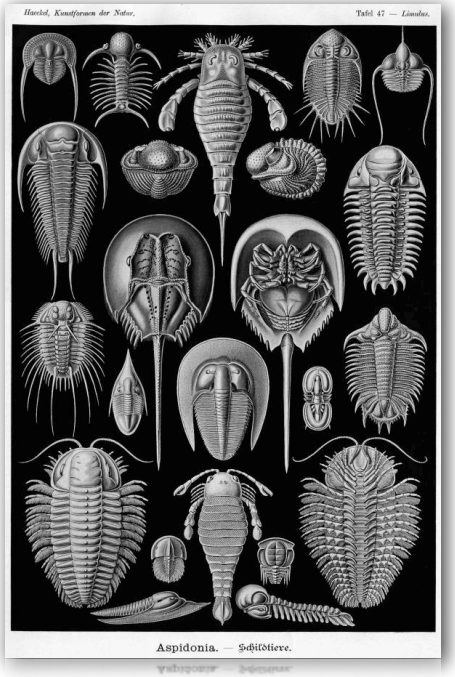
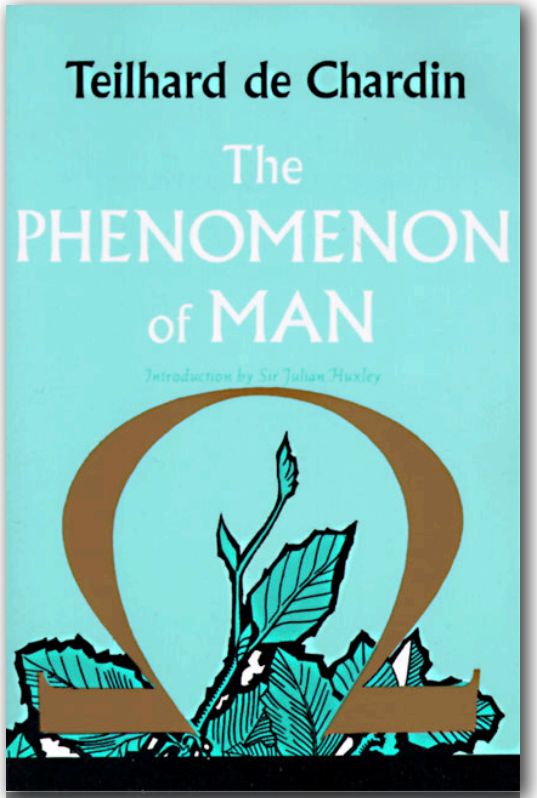
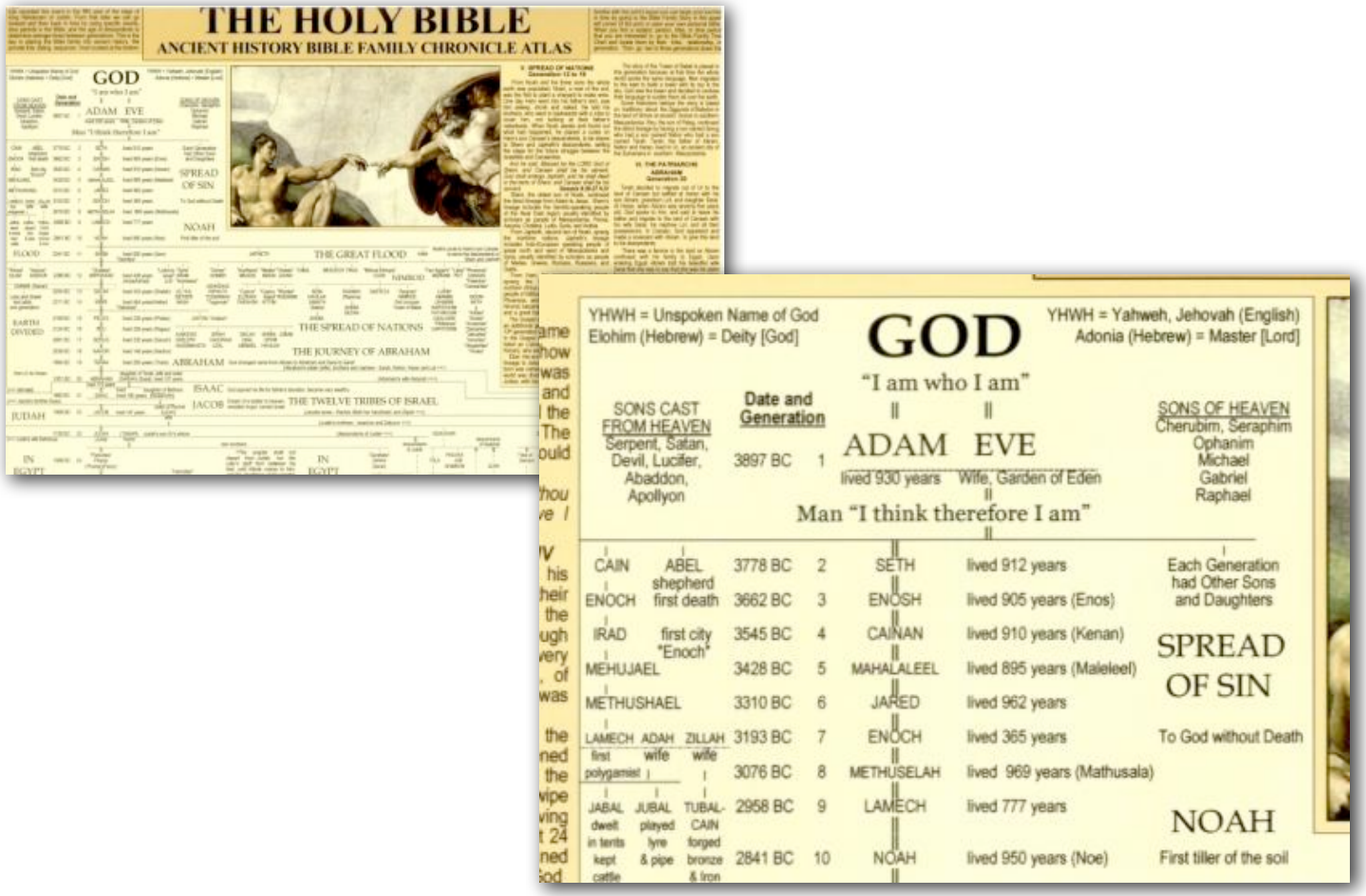
Evolutionary Theory Frontiers?

David Krakauer, Santa Fe Institute




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


THE HOLY BIBLE
ANCIENT HISTORY BIBLE FAMILY CHRONICLE ATLAS
GOD
ADAM EVE
SPREAD OF SIN
NOAH
THE GREAT FLOOD
NIMROD
THE SPREAD OF NATIONS
THE JOURNEY OF ABRAHAM
ABRAHAM
ISAAC
JACOB
THE TWELVE TRIBES OF ISRAEL
JUDAH
EARTH DIVIDED
FLOOD
IN EGYPT
YHWH = Unspoken Name of God
Elohim (Hebrew) = Deity [God]
GOD
"I am who I am"
YHWH = Yahweh, Jehovah (English)
Adonia (Hebrew) = Master [Lord]
SONS CAST FROM HEAVEN
Serpent, Satan, Devil, Lucifer, Abaddon, Apollyon
Date and Generation
3897 BC 1
ADAM EVE
lived 930 years
Wife, Garden of Eden
Man "I think therefore I am"
SONS OF HEAVEN
Cherubim, Seraphim
Ophanim
Michael
Gabriel
Raphael
CAIN
ABEL shepherd first death
3778 BC 2
SETH
lived 912 years
Each Generation had Other Sons and Daughters
ENOCH
first city "Enoch"
3662 BC 3
ENOSH
lived 905 years (Enos)
IRAD
3545 BC 4
CAINAN
lived 910 years (Kenan)
SPREAD OF SIN
MEHUJAEL
3428 BC 5
MAHALALEEL
lived 895 years (Maleleel)
METHUSHAEL
3310 BC 6
JARED
lived 962 years
LAMECH first polygamist
ADAH wife
ZILLAH wife
3193 BC 7
ENOCH
lived 365 years
To God without Death
3076 BC 8
METHUSELAH
lived 969 years (Mathusala)
JABAL dwelt in tents kept cattle
JUBAL played lyre & pipe
TUBAL-CAIN forged bronze & Iron
2958 BC 9
LAMECH
lived 777 years
NOAH
2841 BC 10
NOAH
lived 950 years (Noe)
First tiller of the soil

(tractable) Frontiers in Evolutionary Theory

- Origins of "living systems"
- Origins of complex, hierarchical, adaptive systems - *major transitions & construction*
- Relationship between developmental and evolutionary processes - *evodevo & construction*
- Mechanisms for stabilizing, complex, adaptive lineages - *robustness theories*
- Origins of Culture & Artifacts

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

$$g_i \xrightarrow{d_i} p_i$$

The Assumptions we are going to challenge

Malthusian/Darwinian

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

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

$$g_i \xrightarrow{d_i} p_i$$

Fisherian/Haldanian

ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

CHAPTER I.

VARIATION UNDER DOMESTICATION.

Causes of Variability—Effects of Habit—Correlation of Growth—Inheritance—Character of Domestic Varieties—Difficulty of distinguishing between Varieties and Species—Origin of Domestic Varieties from one or more Species—Domestic Pigeons, their Differences and Origin—Principle of Selection anciently followed, its Effects—Methodical and Unconscious Selection—Unknown Origin of our Domestic Productions—Circumstances favourable to Man's power of Selection.

WHEN we look to the individuals of the same variety or sub-variety of our older cultivated plants and animals, one of the first points which strikes us, is, that they generally differ much more from each other, than do the individuals of any one species or variety in a state of nature. When we reflect on the vast diversity of the plants and animals which have been cultivated, and which have varied during all ages under the most different climates and treatment, I think we are driven to conclude that this greater variability is simply due to our domestic productions having been raised under conditions of life not so uniform as, and somewhat different from, those to which the parent-species have been exposed under nature. There is, also, I think, some probability in the view propounded by Andrew Knight, that this variability may be partly connected with excess of food. It seems pretty clear that organic beings must be exposed during several generations to the new conditions of life to cause any appreciable amount of variation; and that when the organisation has once begun to vary, it generally continues to vary for many generations.

‘Every writer "creates" his own precursors.
His work modifies our conception of the
past, as it will modify the future’

Jorge Luis Borges, Kafka y sus precursores.
Otras Inquisiciones (1952)

STRUCTURE AND DISTRIBUTION

OF

CORAL REEFS.

BEING THE FIRST PART OF
THE GEOLOGY OF THE VOYAGE OF THE BEAGLE,
UNDER THE COMMAND OF CAPT. FITZROY, R.N.
DURING THE YEARS 1832 TO 1836.

BY

CHARLES DARWIN, M.A., F.R.S., F.G.S.,
NATURALIST TO THE EXPEDITION.

Published with the Approval of the Lords Commissioners of
Her Majesty's Treasury.

LONDON:
SMITH, ELDER AND CO., 65, CORNHILL.
1842.

THE FORMATION

OF

VEGETABLE MOULD,

THROUGH THE

ACTION OF WORMS.

WITH

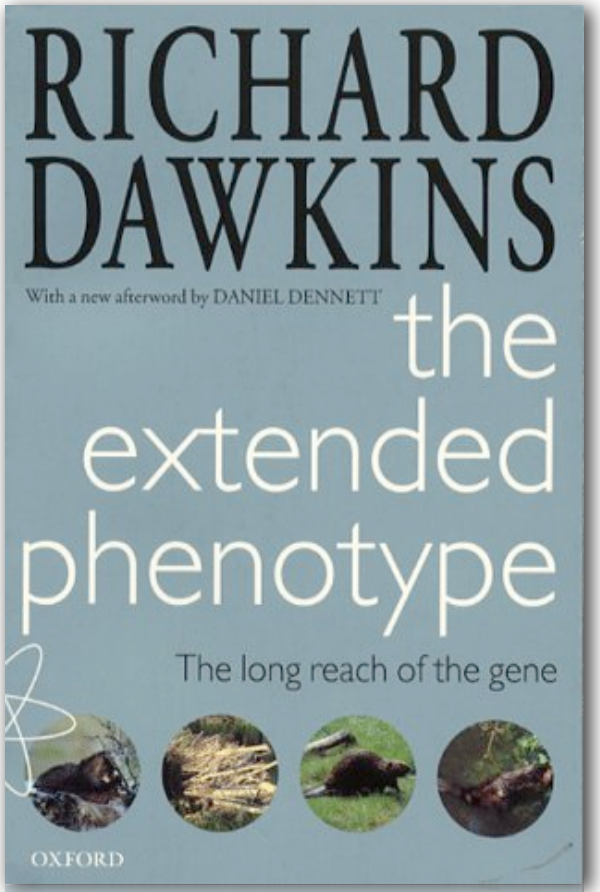
OBSERVATIONS ON THEIR HABITS.

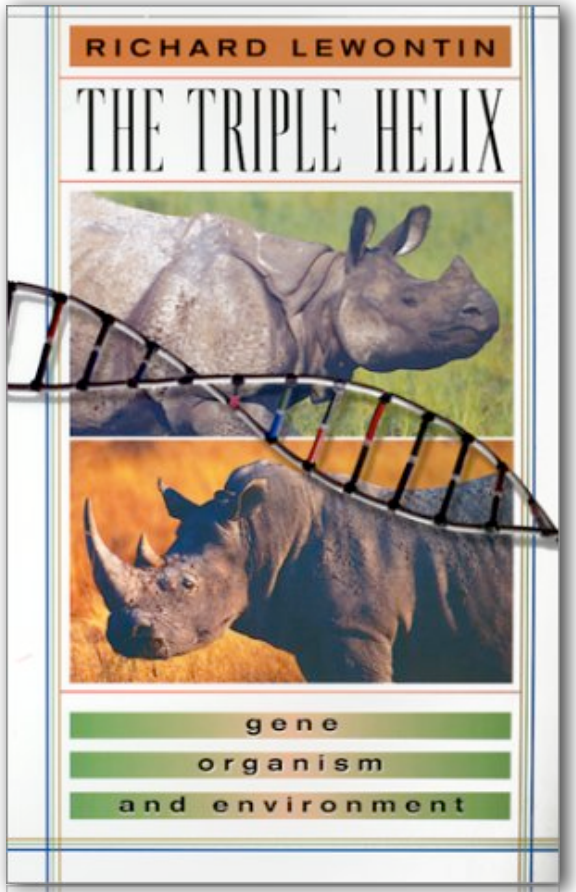
By CHARLES DARWIN, LL.D., F.R.S.

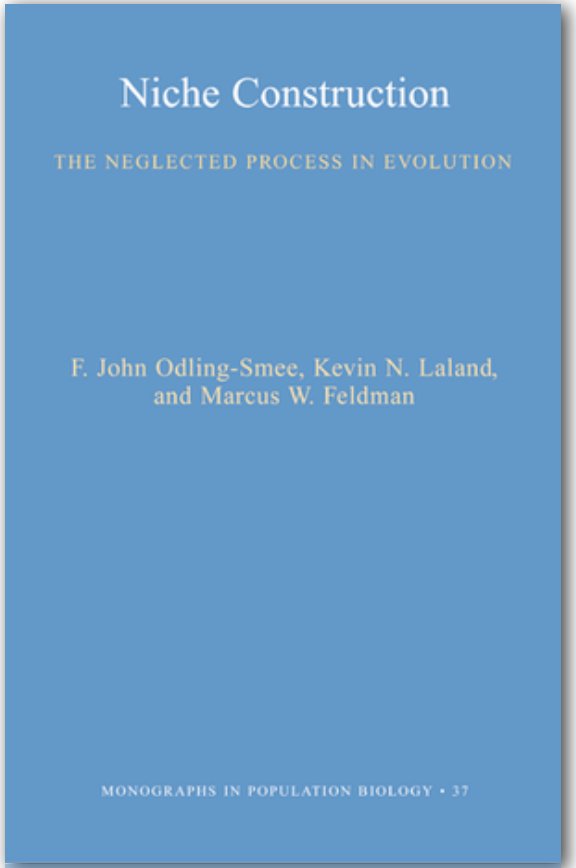
WITH ILLUSTRATIONS.

SEVENTH THOUSAND (CORRECTED)

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1882.


RICHARD
DAWKINS
With a new afterword by DANIEL DENNETT
the
extended
phenotype
The long reach of the gene
OXFORD


RICHARD LEWONTIN
THE TRIPLE HELIX
gene
organism
and environment


Niche Construction
THE NEGLECTED PROCESS IN EVOLUTION
F. John Odling-Smee, Kevin N. Laland,
and Marcus W. Feldman
MONOGRAPHS IN POPULATION BIOLOGY • 37

“It is vain to talk of the interest of the community, without understanding what is the interest of the individual”

Jeremy Bentham

“Society exists only as a mental concept; in the real world there are only individuals.”

Oscar Wilde.

“Everyone thinks of changing the world, but no one thinks of changing himself”.

Leo Nikolaevich Tolstoy

Niche Construction

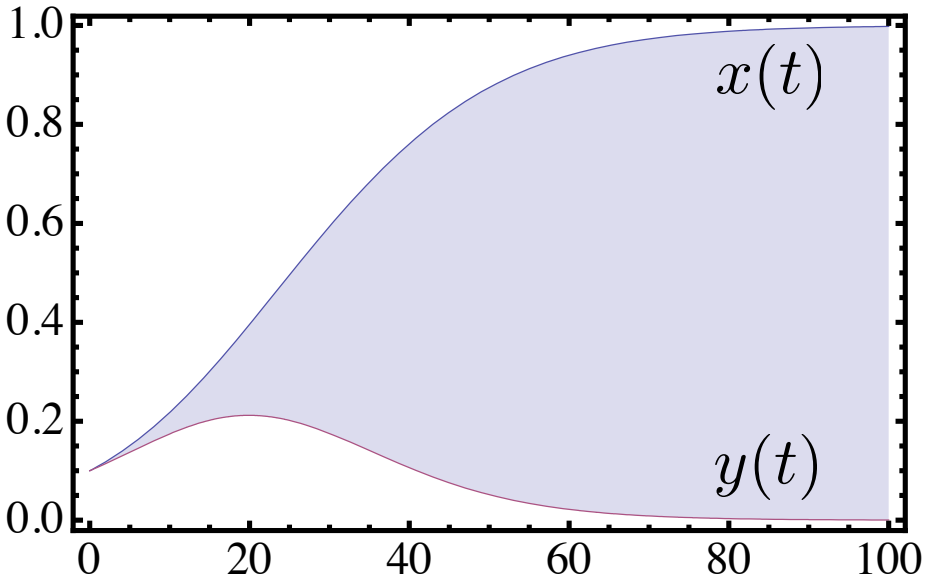
The Niche

- Grinnel (1917) - many environmental variable foraging recess *(den. dep)*
- Elton (1927) - Grinnel + inclusion of interactions among species *(freq. dep.)*
- Hutchinson (1959) - high dimensional space of combined organism-environment interactions
- Niche Construction - how the adaptive complement of above come into existence

Ecological Dynamics

$$\dot{x} = c_x x - x\frac{x + b_{yx} y}{k_x}$$

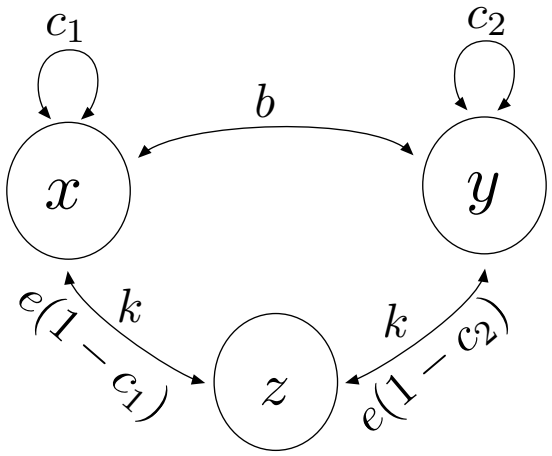
$$\dot{y} = c_y y - y\frac{y + b_{xy} x}{k_y}$$



$b_{yx} < b_{xy}$

Niche Construction Dynamics

Perhaps take a look at: Krakauer et al. Am. Nat. 2009



$$\dot{x} = c_x x - x\frac{x + b_{yx}y}{k_x z} \tag{1}$$

$$\dot{y} = c_y y - y\frac{y + b_{xy}x}{k_y z} \tag{2}$$

$$\dot{z} = p + (1 - c_x)\frac{ex}{x + y + z} + (1 - c_y)\frac{ey}{x + y + z} - dz. \tag{3}$$

Implications

- Genome encodes components of the environment
- Possibility of greater abundance (a)
- Increased stability (s)
- Increased specialization/division of labor (l)
- Increased diversity (d)
- Increased complexity (e,g, kd^2, ld)

However there is a Problem!

$$\dot{x} = cx - x\frac{x+w}{kz},$$

$$\dot{w} = c'w - w\frac{w+x}{kz},$$

$$\dot{z} = p + (1-c)\frac{ex}{x+w+z} + (1-c')\frac{ew}{x+w+z} - dz.$$

$$\frac{\dot{w}}{w} = \frac{\dot{x}}{x} + (c'-c)$$

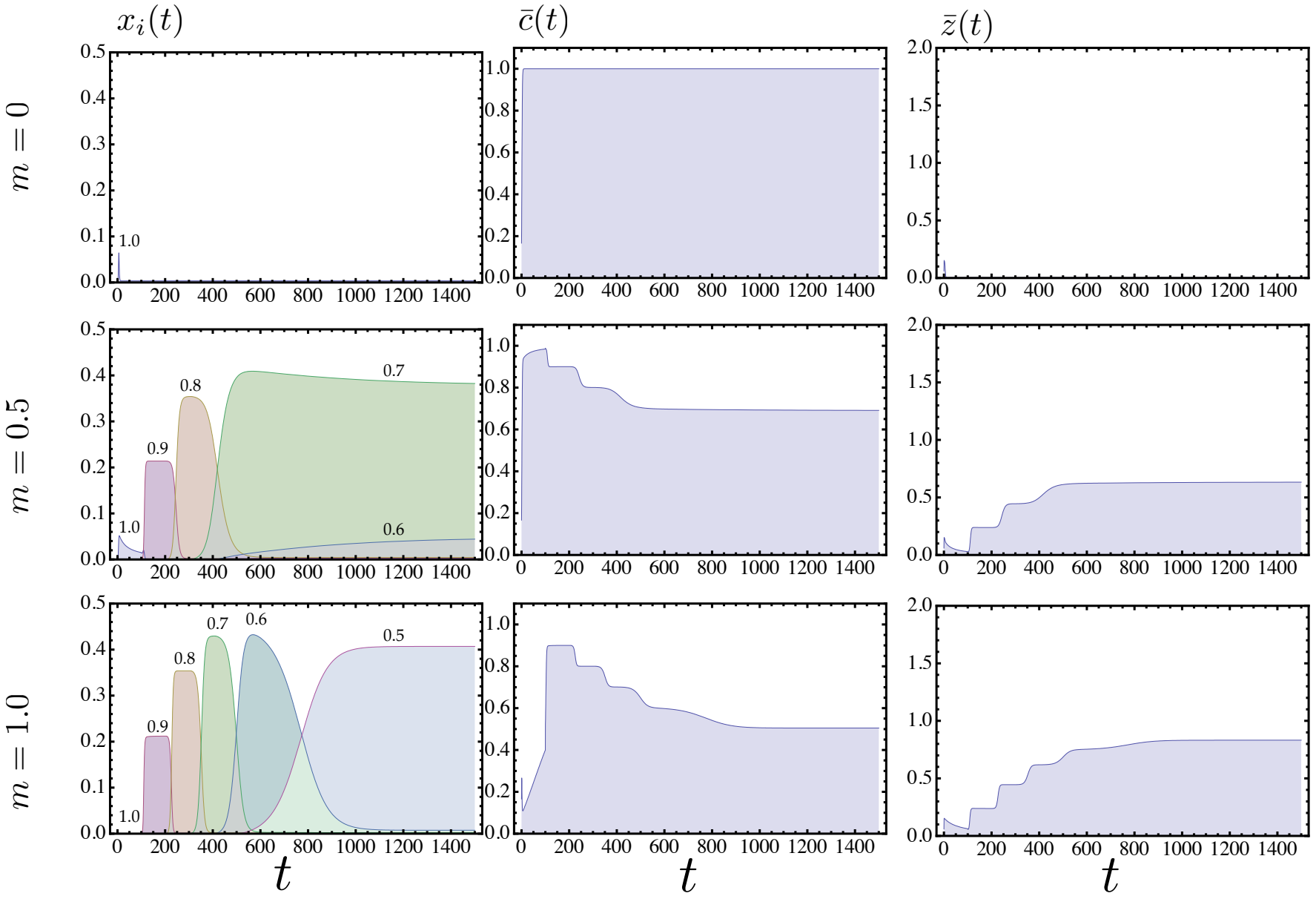
$$\frac{w}{w(0)} = \frac{x}{x(0)}e^{(c'-c)t}.$$

Nevertheless...

Stability of construction monopolized niches

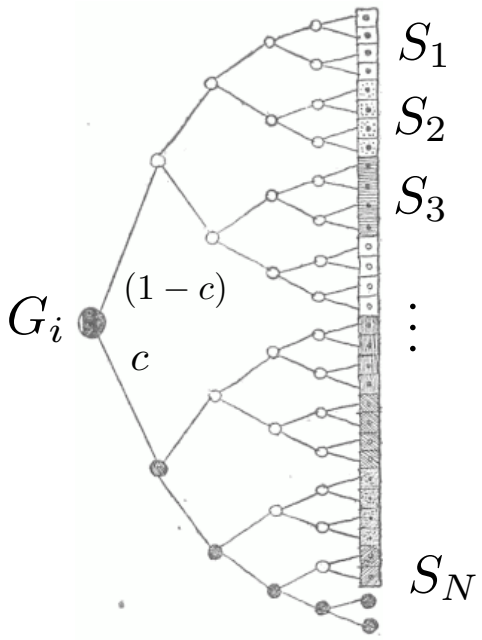
$$z_x \approx z_x m + z_x(1-m)$$

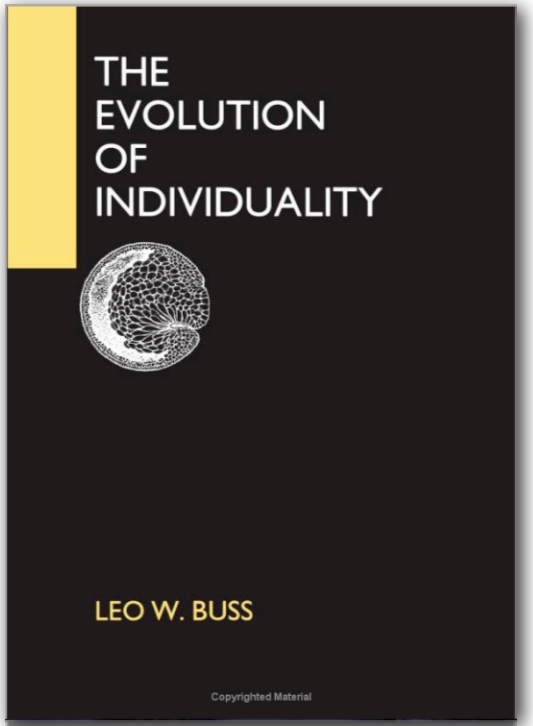
Consider a population of lineages that vary in the value of c_x and m.

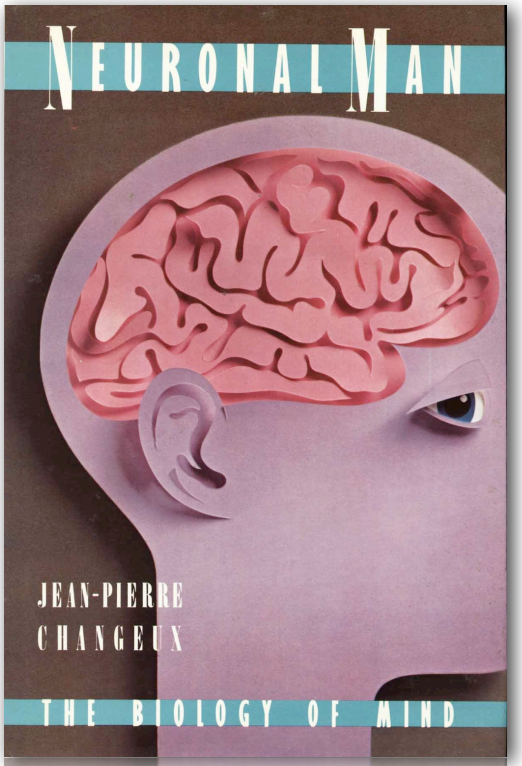

$x_i(t)$
$\bar{c}(t)$
$\bar{z}(t)$
$m = 0$
$m = 0.5$
$m = 1.0$
1.0
0.9
0.8
0.7
0.6
0.5
t
t
t

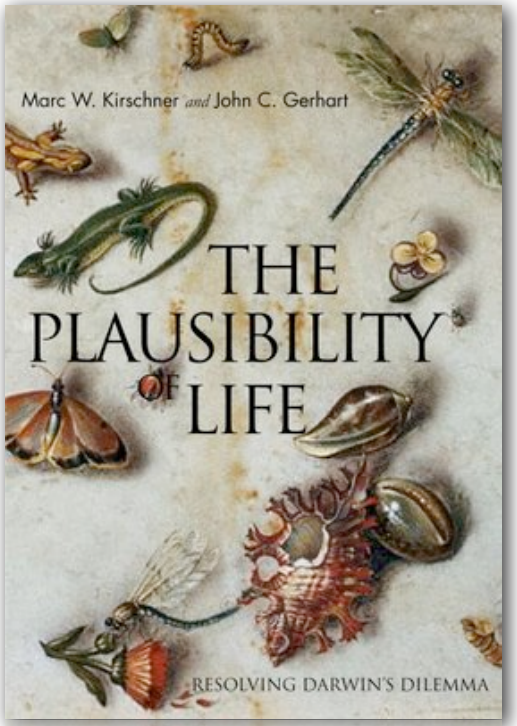
Niche Constructing Development

Organismal development




THE
EVOLUTION
OF
INDIVIDUALITY
LEO W. BUSS
Copyrighted Material


NEURONAL MAN
JEAN-PIERRE
CHANGEUX
THE BIOLOGY OF MIND


Marc W. Kirschner and John C. Gerhart
THE
PLAUSIBILITY
OF
LIFE
RESOLVING DARWIN'S DILEMMA

$$G + R \xrightarrow{r + pkS} 2G$$

$$G + R \xrightarrow{(1-p)k} G + S$$

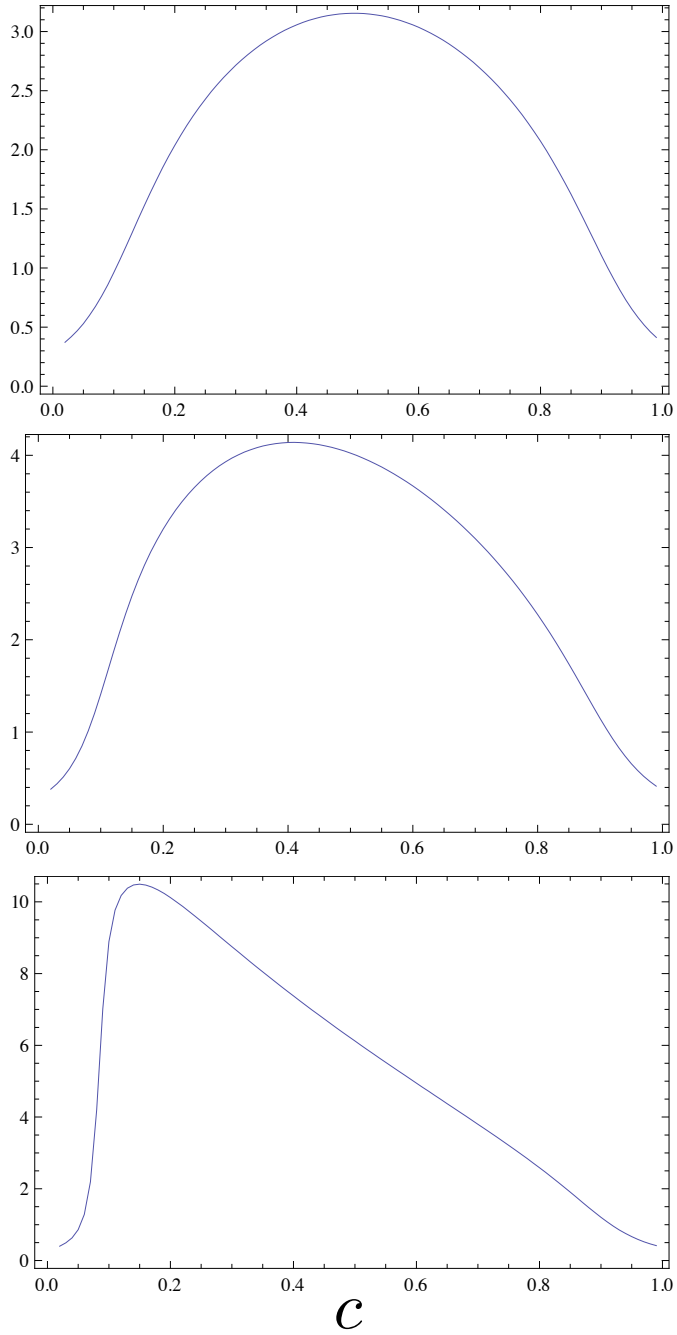
$$2S \xrightarrow{c} S$$

$$\theta \xrightarrow{k + nS} R \qquad R \xrightarrow{d} 0$$

small *n*

mid *n*

large *n*



Symmetric division

Asymmetric division

Perhaps a little too simple?

$$G + R \rightarrow G + S$$

Need to specify a developmental program

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

Evolutionary Implications of Developmental Programs

Perhaps take a look at: Borenstein & Krakauer Plos. Comp. Biol. 2009

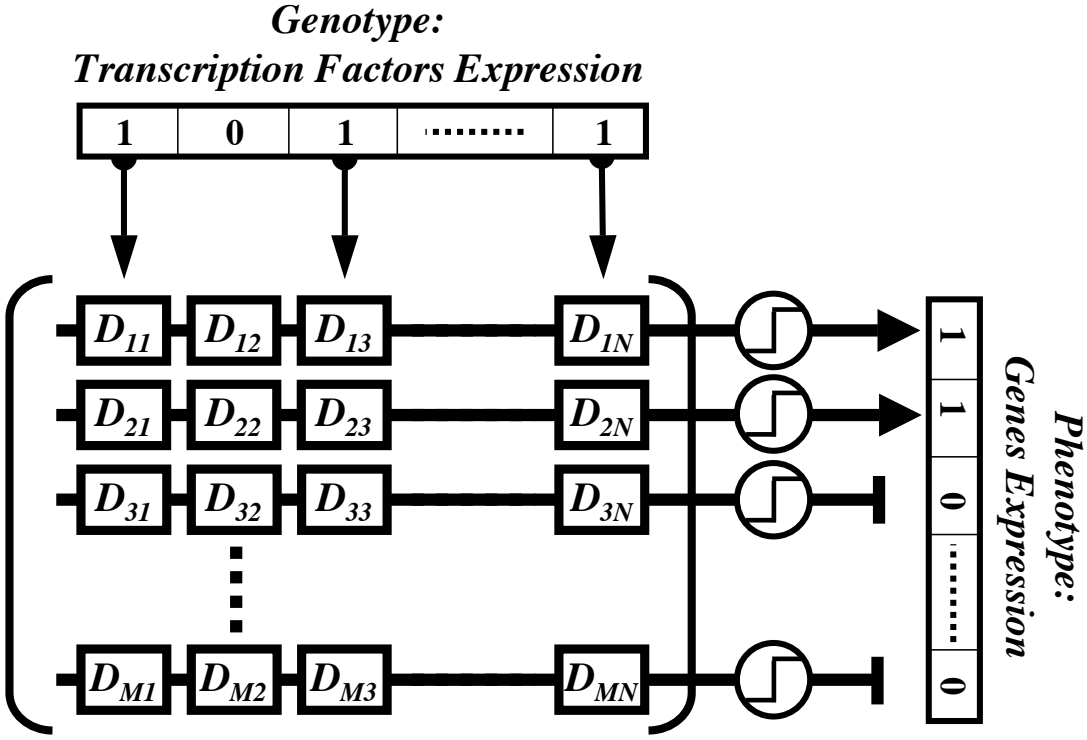
“Frontier” Issues in EvoDevo

- Putative sparseness of the morphospace (many to one property)

The Star Trek multiverse Bauplan

Key Theory Issues in EvoDevo

- Putative sparseness of the morphospace (many to one property)
- Violations of phenotypic isotropy
- Deviations from uniformitarianism (the cambrian disparity)
- Convergence is surprisingly frequent
- Morphological evolution guided by regulatory genes rather than structural



$$p(D_{ij} = +1 | c_{ij} = 1) = q \qquad \vec{p} = H(D\vec{g})$$

Single Projection

$$\vec{p} = H(D\vec{g})$$

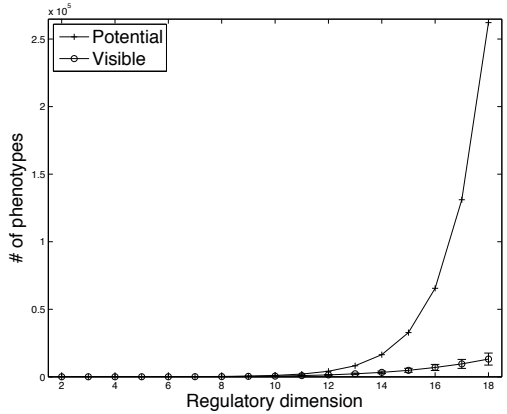
Recurrent Projection

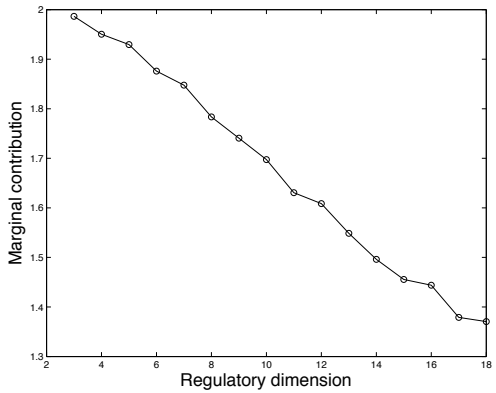
$$\vec{p_t} = H(D\vec{p}_{t-1})$$

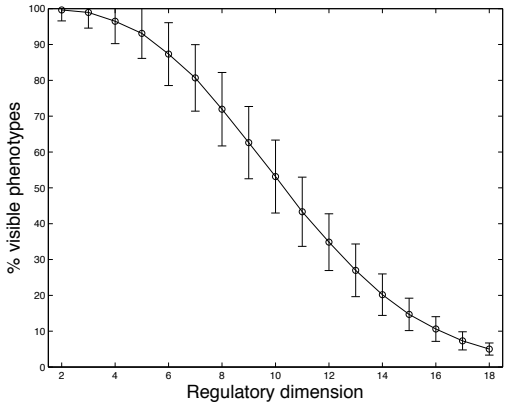
Recurrent Random Projection

$$\vec{p_t} = H(D_t\vec{p}_{t-1})$$

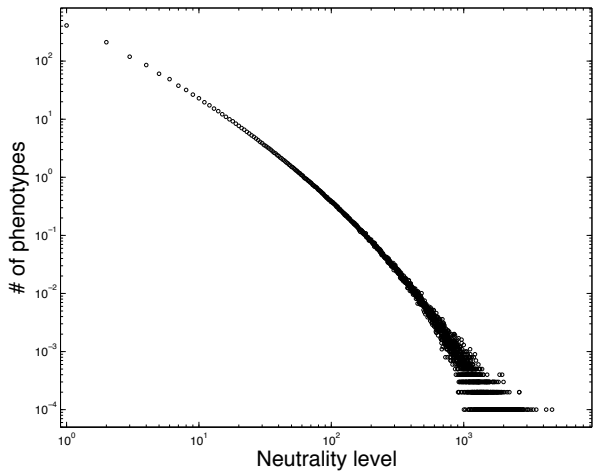
Hidden Phenotypes

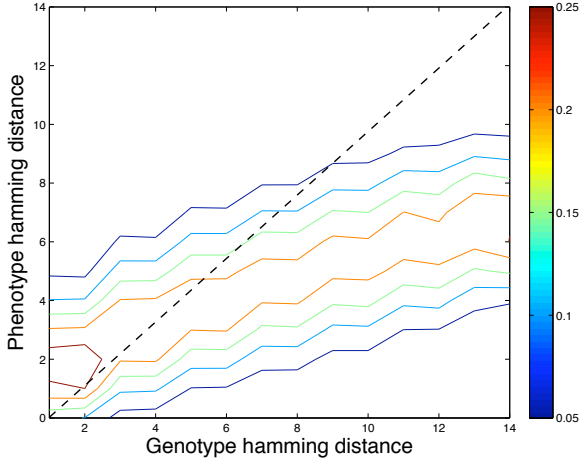

x 10^5
Potential
Visible
# of phenotypes
Regulatory dimension

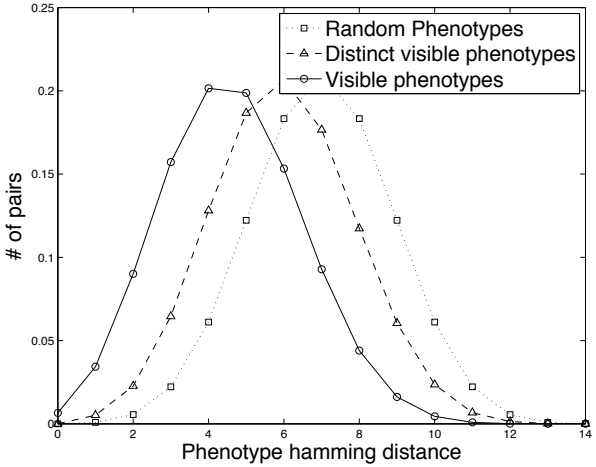

Marginal contribution
Regulatory dimension


% visible phenotypes
Regulatory dimension

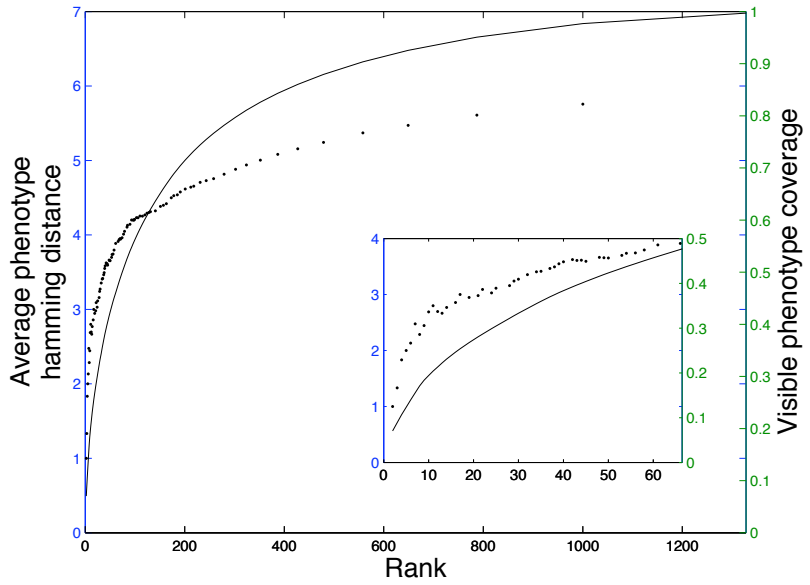
Localization of visible sub-space

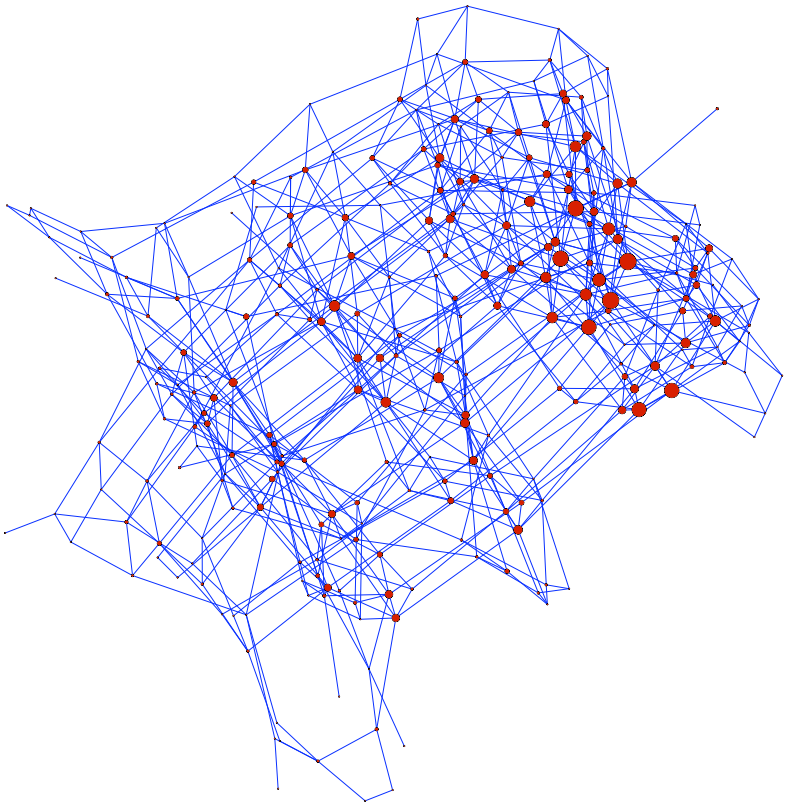

# of phenotypes
Neutrality level


Phenotype hamming distance
Genotype hamming distance


Random Phenotypes
Distinct visible phenotypes
Visible phenotypes
# of pairs
Phenotype hamming distance

Structure of visible sub-space


Average phenotype
hamming distance
Visible phenotype coverage
Rank
0
200
400
600
800
1000
1200
0
1
2
3
4
5
6
7
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
10
20
30
40
50
60



Hierarchical Projections:

Recurrent Projection

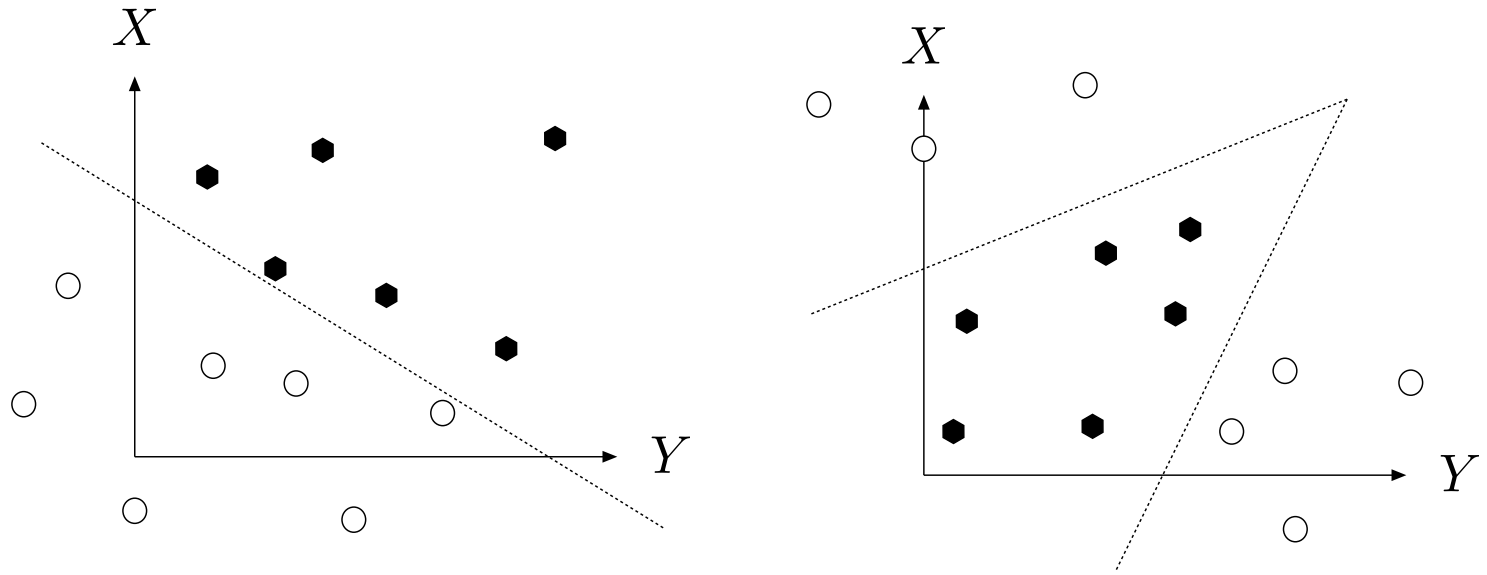
$$\vec{p_t} = H(D\vec{p}_{t-1})$$

Recurrent Random Projection

$$\vec{p_t} = H(D_t\vec{p}_{t-1})$$

Some Connections (for the fastidious)

Linear & Polyhedral separability of activation patterns in phenotypic feature space



Computational complexity issues

- NP-complete to determine polyhedral separability of 2 sets of points
- NP-complete to determine whether k-lines can separate 2 sets
- For k lines polynomial time to determine whether sets are separable

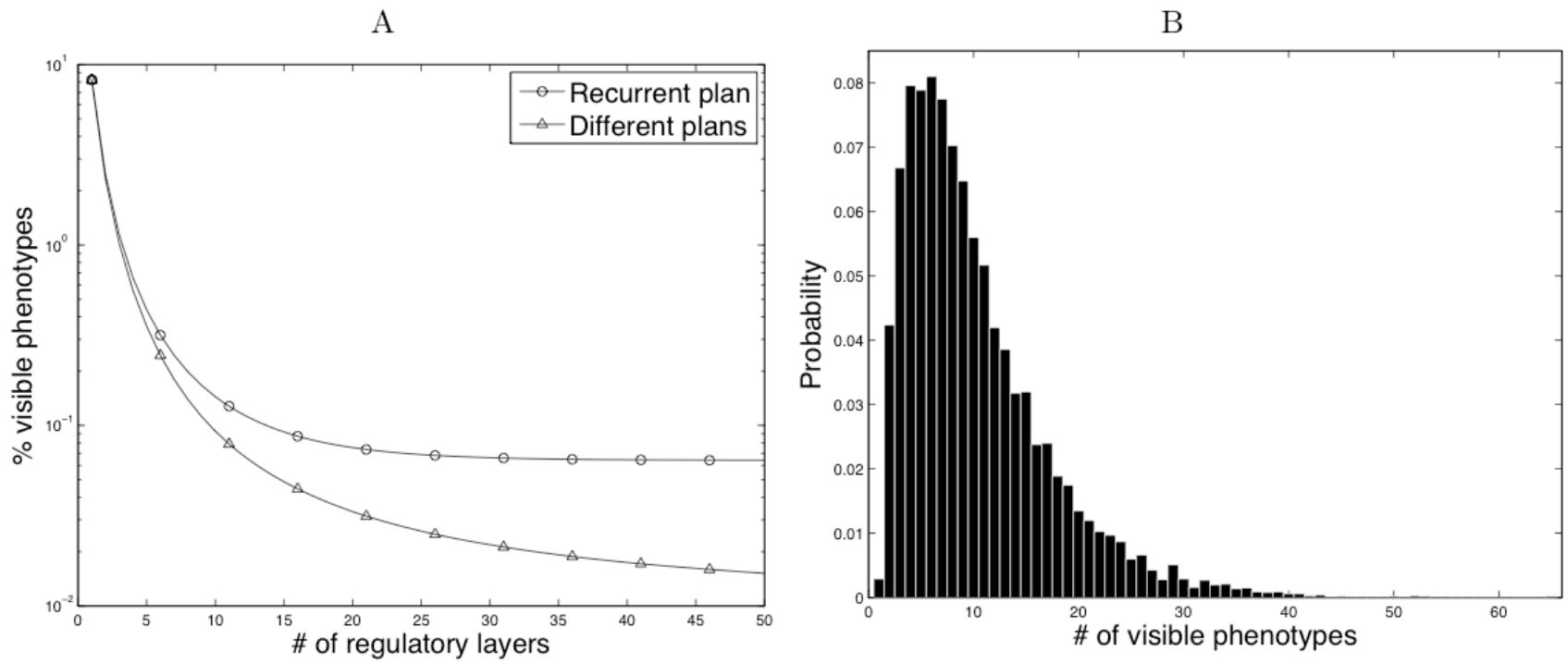
Cybenko Theorem:
universal function approximation
with superpositions of sigmoids

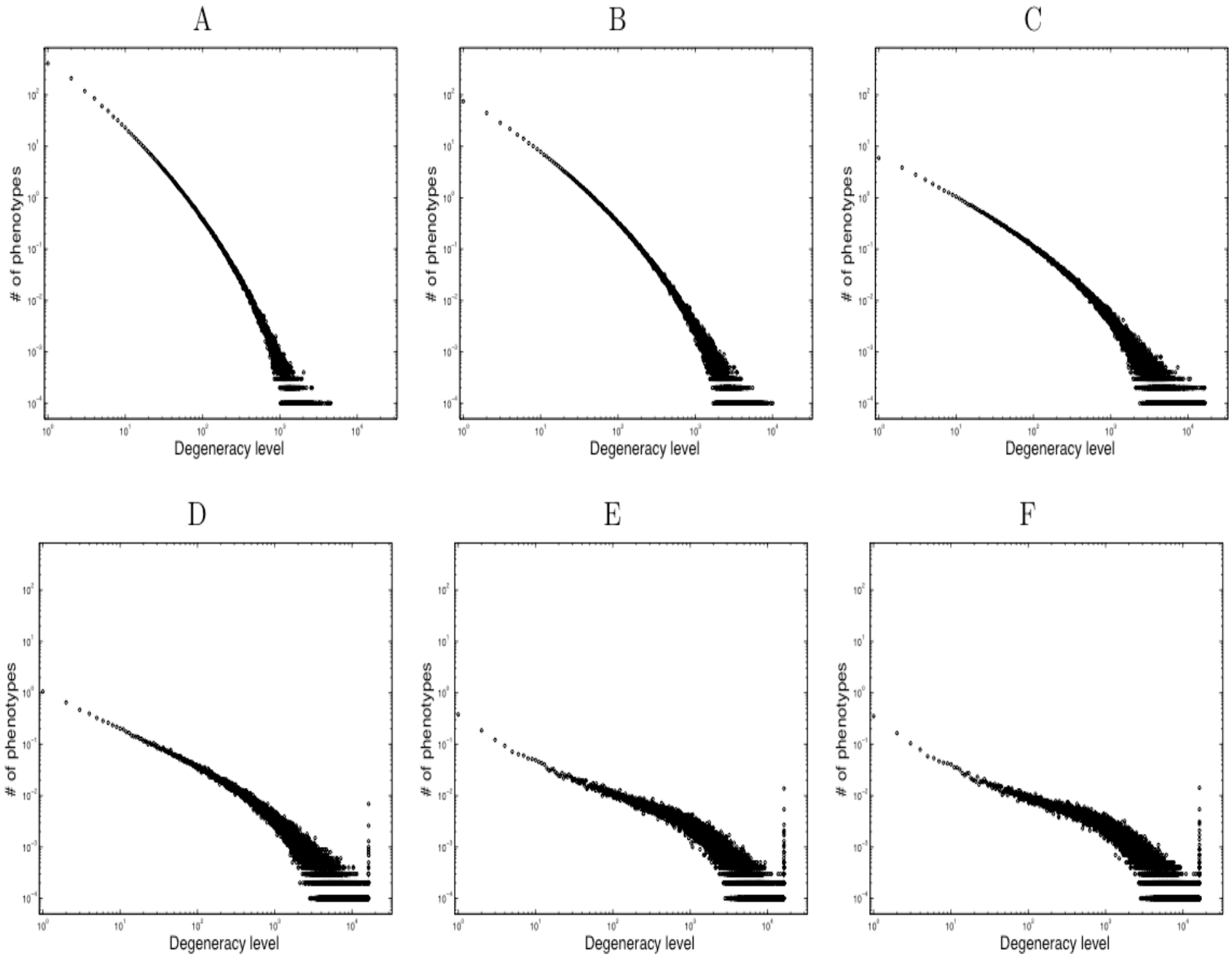
$$G(\mathbf{x}, \mathbf{w}, \alpha, \theta) = \sum_{\mathbf{i=1}}^{\mathbf{N}} \alpha_{\mathbf{i}} \sigma(\mathbf{w_i^T x} + \theta_{\mathbf{i}})$$

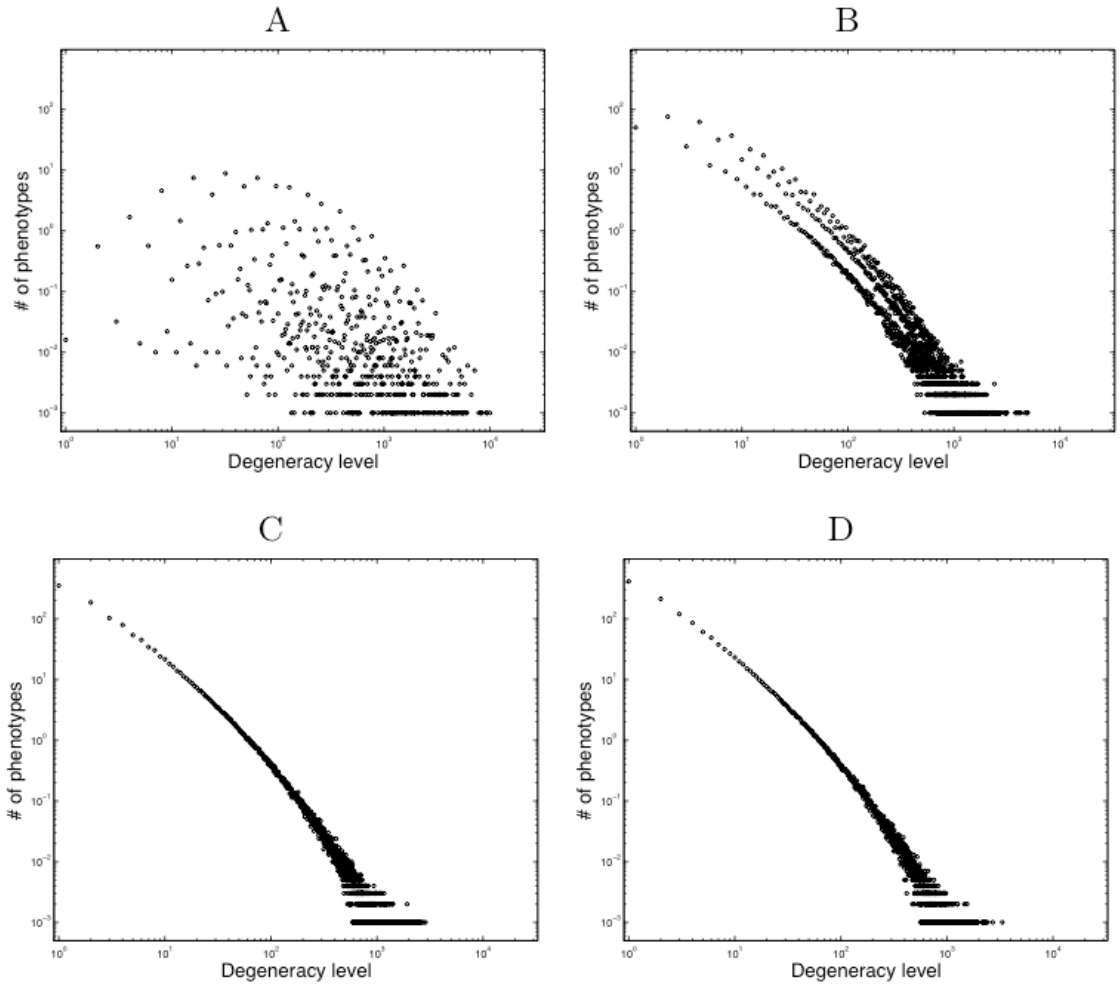
$$|G(\mathbf{x}, \mathbf{w}, \alpha, \theta) - f(x)| < |\epsilon|, \mathbf{x} \in [\mathbf{0}, \mathbf{1}]^{\mathbf{n}}$$

Random Matrix (products) Theory

- Products of random matrices essential in chaotic dynamics
- In d=1 case, limiting distribution of random products, log(X)
- Problems of non-commutativity of matrix
- Infinite products of 2 by 2 linear projections is a solved problem.

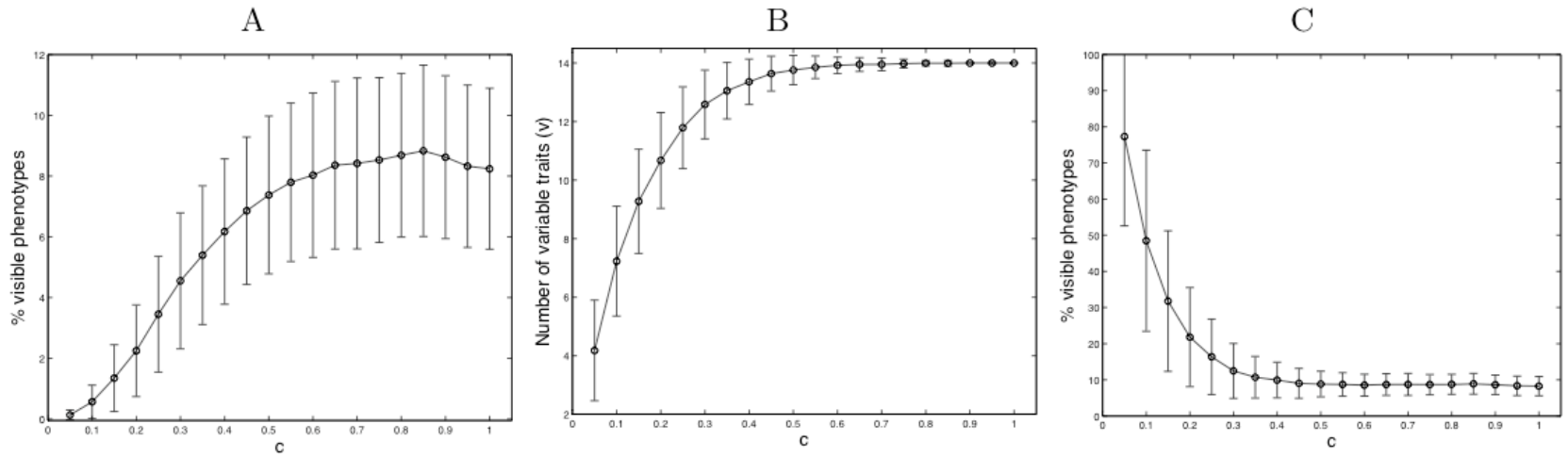

A
B
Recurrent plan
Different plans
% visible phenotypes
# of regulatory layers
Probability
# of visible phenotypes


A
B
C
D
E
F
# of phenotypes
Degeneracy level


A
B
C
D
# of phenotypes
Degeneracy level

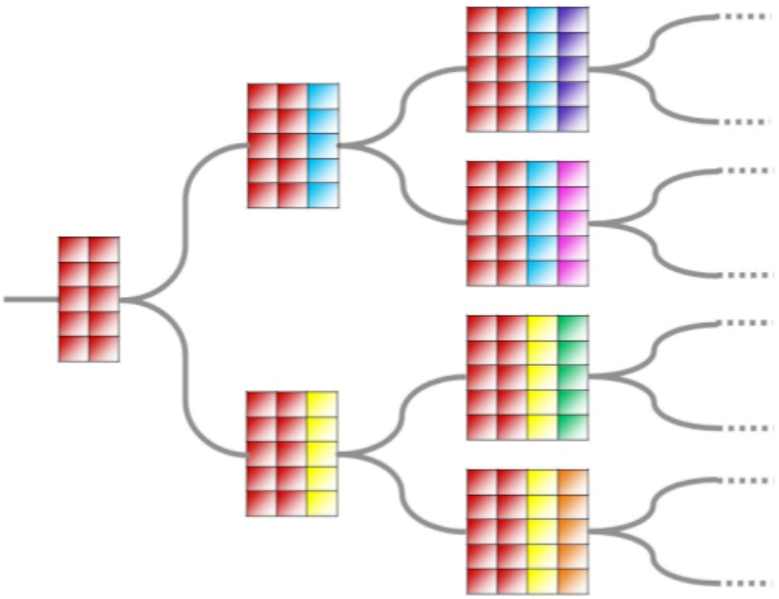
Sparseness: freedom or constraint?

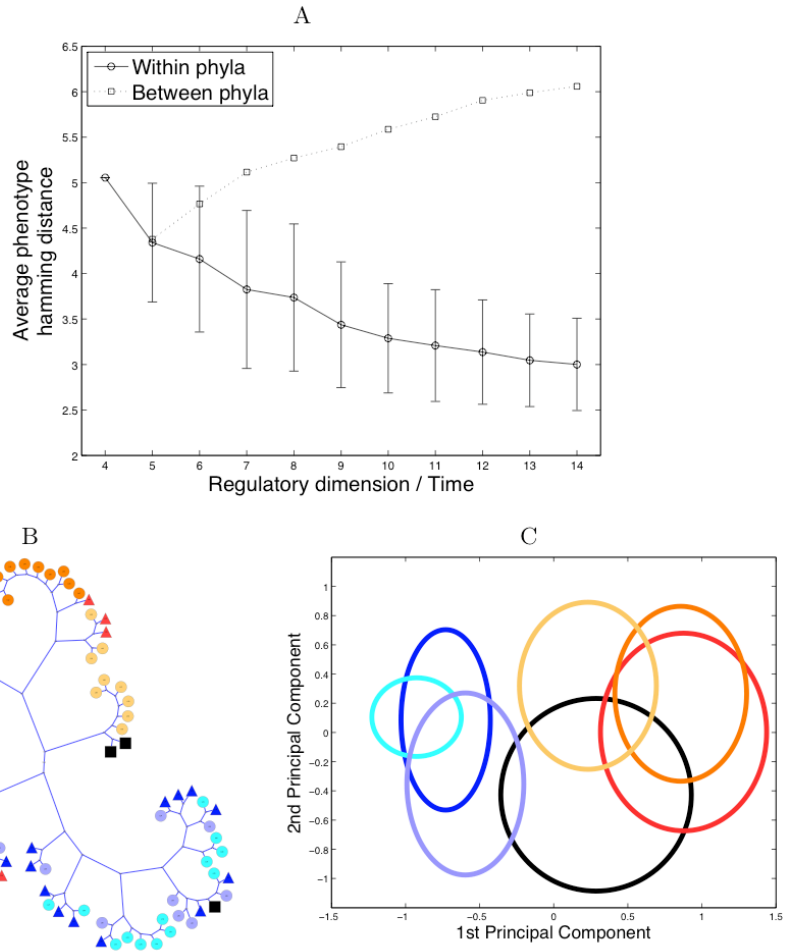
The Origins of Regulatory Freedom


A
% visible phenotypes
c
B
Number of variable traits (v)
c
C
% visible phenotypes
c

Developmental Evolution

Take a look at: Borenstein & Krakauer Plos. Comp. Biol. 2009




A
Within phyla
Between phyla
Average phenotype hamming distance
Regulatory dimension / Time
B
C
2nd Principal Component
1st Principal Component

Frontiers

- Niche construction allows us to explore the origins of hierarchical selective system
- Development (& the organism) is seen to be a special form of "contracted" ecological dynamic
- Development has a more "programmed" character
- Some Implications of cis-regulatory programs are:
- Most phenotypes are inaccessible
- Visible phenotypes tend to be alike (convergence not rare)
- Low regulatory dimension generates high disparity but low diversity.

The Future

- A unified evolutionary theory of organism and environment & hence a *theory of selection (of semantics)*
- Generalization of aspects of the general theory to culture
- A more constructive framework for studying all forms of high memory-capacity adaptive dynamics

Select Bibliography

FJ Odling-Smee, KN Laland, MW Feldman. Niche Construction: The Neglected Process in Evolution. 20003.

Krakauer, D.C., Page, K. and Erwin.D. Diversity, Dilemmas and Monopolies of Niche Construction. Am. Nat. (2009)

Borenstein, E. Krakauer, D.C. End to Endless Forms: Regulatory Epistasis, Phenotype Distribution Bias, and Non-Uniform Evolution. PloS. Comp. Biol. 4. 1-13. e1000202. (2008).

Bershad, A.K., Fuentes, M.A, Krakauer, D.C. Developmental autonomy and somatic niche construction during cellular division and differentiation. J. theor. Biol. 254. 408-416. (2008).

Ay, N. & Krakauer, D.C. Geometric Robustness Theory and Biological Networks. Theory in the Biosciences. 125(2), 93-121. (2007)