Evolutionary Transitions and Top-Down Causation

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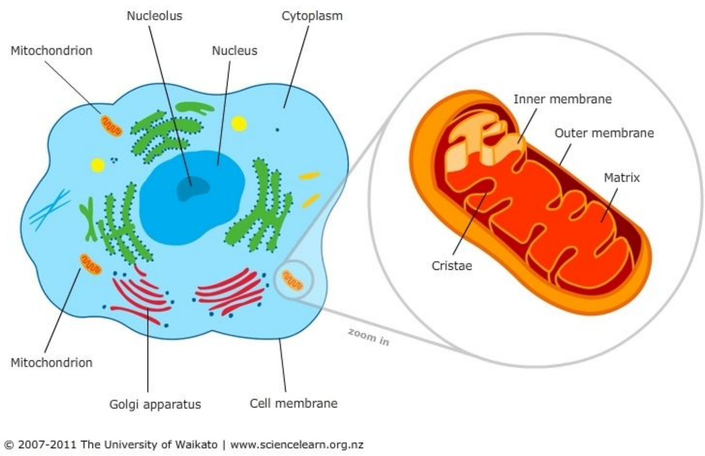
Top-down causation has been suggested to occur at all scales of biological organization as a mechanism for explaining the hierarchy of structure and causation in living systems (Campbell,1974; Auletta et al., 2008; Davies, 2006b, 2012; Ellis,2012).

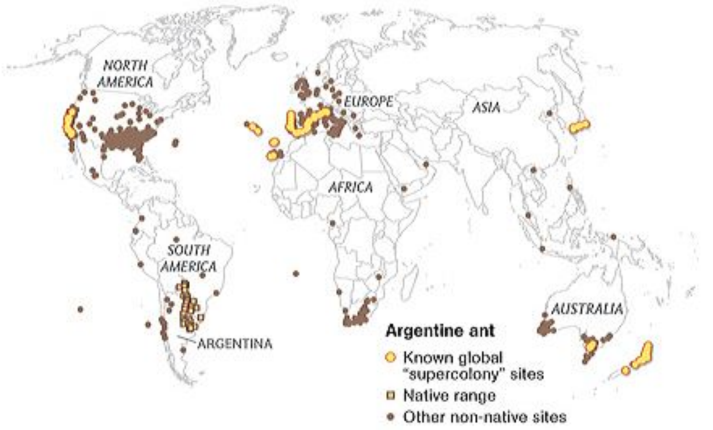
Here we propose that a transition from bottom-up to top-down causation – mediated by a reversal in the flow of information from lower to higher levels of organization, to that from higher to lower levels of organization – is a driving force for most major evolutionary transitions. We suggest that many major evolutionary transitions might therefore be marked by a transition in causal structure.

We use logistic growth as a toy model for demonstrating how such a transition can drive the emergence of collective behavior in replicative systems. We then outline how this scenario may have played out in those major evolutionary transitions in which new, higher levels of organization emerged, and propose possible methods via which our hypothesis might be tested.

Major Evolutionary Transitions

- from non-coded to coded information
  - (the origin of the genetic code)
- from prokaryotes to eukaryotes
  - Cells with a nucleus
- from protists (single cells) to multicellular organisms
- from primate groups to linguistic communities
- And I would add
  - From individual insects to eusocial insect colonies, and possibly unicolonial "super colonies"
  - From evolution between generations to evolution within individual lifespans (adaptive immunity)

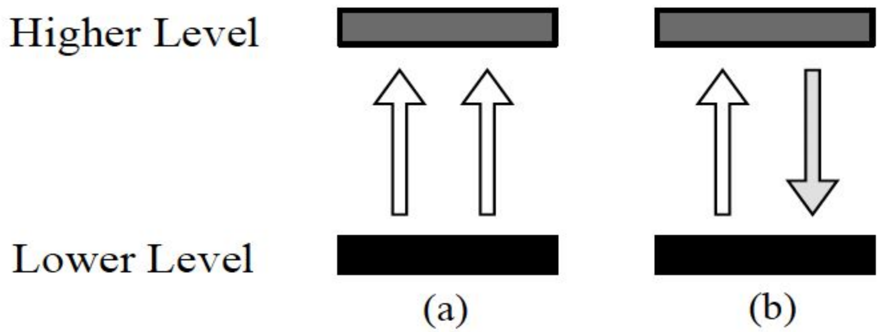




Introduction

- What "universal principles underlie such large jumps in biological complexity"?
  - Parts loose their autonomy (mitochondria can't replicate on their own)
  - changes in the way information is stored and transmitted (necessary, not sufficient)
    - e.g. epigenetics (multiple phenotypes from the same genotype) allowed differentiation required for multicellular plants and animals
  - What mechanisms allow higher levels of organization to emerge?
    - They propose: "**information gaining causal efficacy** over higher levels of organization."
    - "a transition to top-down causation via informational efficacy over new, higher levels of organization might enable the emergence of higher-level entities."
- "A reversal in the dominant direction of information flow, from bottom-up to top-down, is correlated with the emergence of collective behavior in replicative systems".
  - They hypothesize that this drove the origin of life and multicellularity

Informational Efficacy and Top-Down Causation



- a) The standard (reductionist) view suggests everything in the universe is directed by bottom-up action only, such that causation flows strictly from lower to higher levels.

- b) Biological organization suggests higher levels of organization modify the causal relations below via top-down causation.

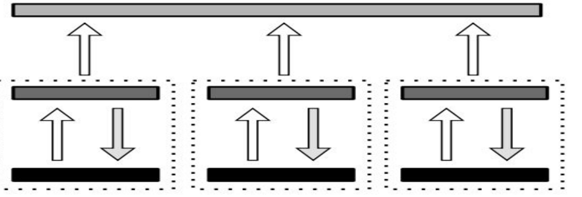
- The rules of the game change over time
- Biological information
  - is contextual and *means* something;
  - has *efficacy*: it does something useful

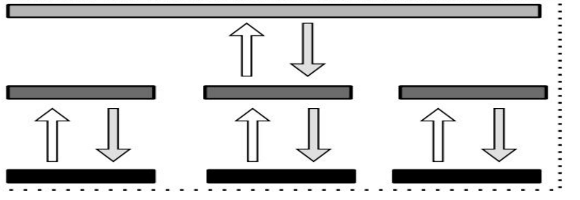
It is the efficacy of information that leads to the convolution of dynamical laws and states that makes biology so unique.

This convolution results in multidirectional causality with causal influences running both up and down the hierarchy of structure of biological systems (e.g. both from genome to proteome, and from proteome to genome via the switching on and off of genes.

Evolutionary transitions should be characterized by a transition from bottom-up to top-down causation, mediated by a reversal in the dominant direction of information flow.

They test this by measuring transfer entropy in a logistic map "toy model"


(a)


(b)

Logistic Growth as a Toy Model

- an analogy with the transition from independent replicators to collective reproducers
- Show how a reversal in dominant information flow (transfer entropy) describes the emergence of a new collective entity

$$x_{i,n+1} = (1 - \epsilon) f_i(x_{i,n}) + \epsilon\, m_n \quad ; \quad (i = 1, 2, \ldots N) \quad (1)$$

- epsilon is the global coupling strength to the mean population

$$f_i(x_{i,n}) = r_i x_{i,n} \left(1 - \frac{x_{i,n}}{K}\right) \quad (2)$$

- f_i is the logistic map for subpopulation *i*

$$x_{i,n+1} = (1-\epsilon) f_i(x_{i,n}) + \epsilon\, m_n ; \quad (i = 1, 2, \ldots N) \quad (1)$$

- epsilon is the global coupling strength to the mean population

$$f_i(x_{i,n}) = r_i x_{i,n} \left(1 - \frac{x_{i,n}}{K}\right) \quad (2)$$

- x_0 is 1; r is in the chaotic range [3.9,4.0]

$$M_n = \frac{1}{N} \sum_{j=1}^{N} x_{j,n} \quad (3)$$

- State of the whole global population

$$m_n = \frac{1}{N} \sum_{j=1}^{N} f_j(x_{j,n}) \quad (4)$$

- Dynamics of the whole global population

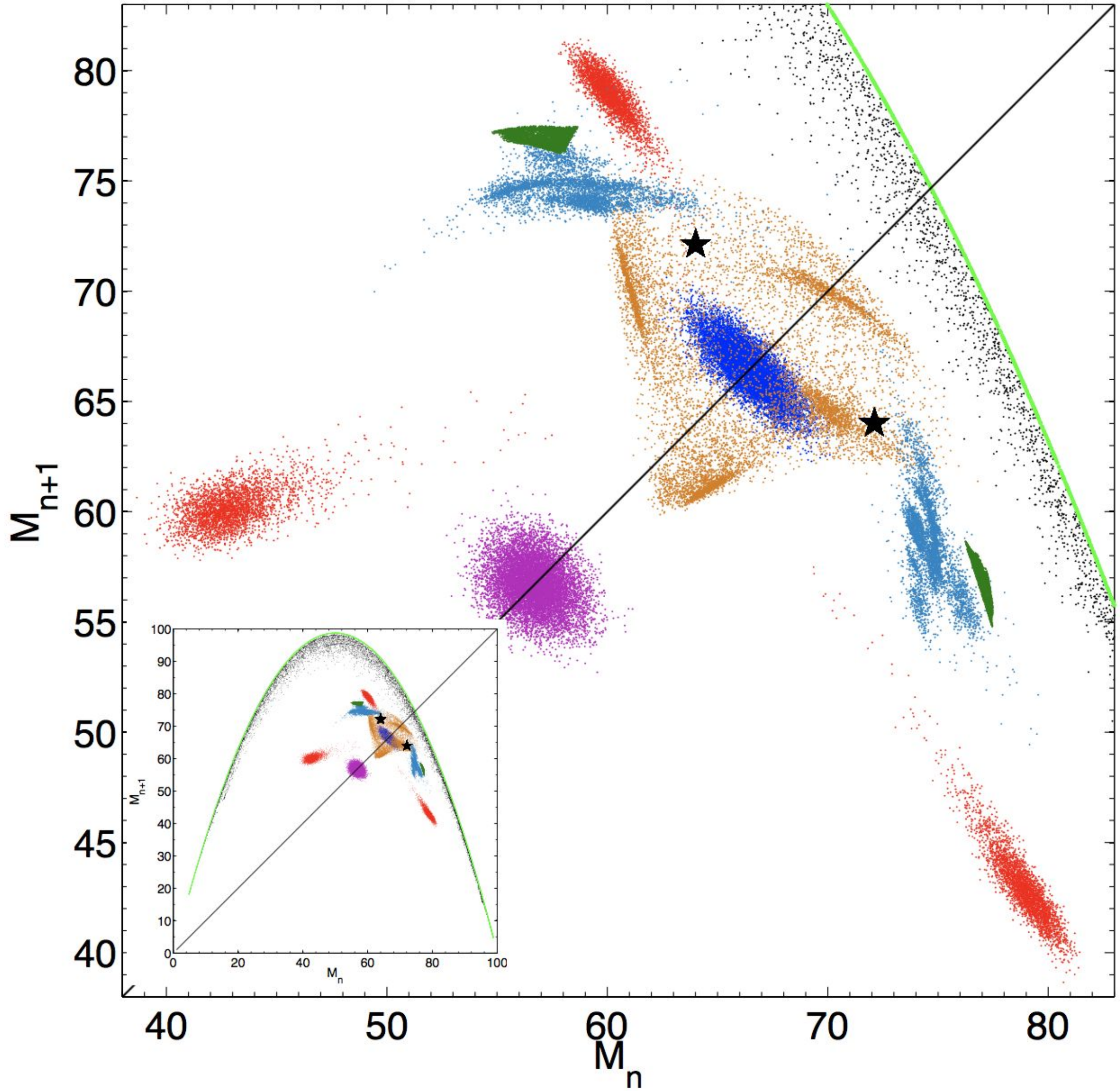


Figure 3: Return map for varying values of the global coupling strength ϵ. Shown are return maps for $\epsilon = 0$ (magenta), $\epsilon = 0.075$ (red), $\epsilon = 0.1$ (blue), $\epsilon = 0.2$ (orange), $\epsilon = 0.225$ (aqua), $\epsilon = 0.25$ (dark green), $\epsilon = 0.3$ (stars), and $\epsilon = 0.4$ (black). Also shown is the return map for a single logistic map (bright green). The inset shows an expanded view.

1000 maps
10,000 time steps

Compare M to a randomly chosen population, X:

$$T_{X \to M}$$

$$T_{M \to X}$$

Quantify Information transfer between local and global populations using Transfer Entropy

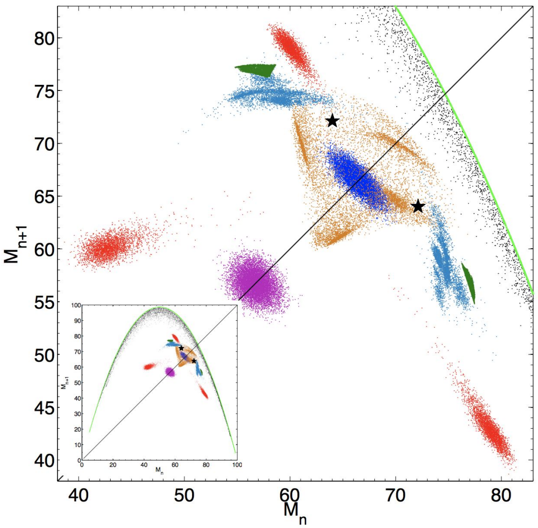
$$T_{Y\to X}^{(k)} = \sum_n p(x_{n+1}, x_n^{(k)}, y_n^{(k)}) \log \left[\frac{p(x_{n+1}|x_n^{(k)}, y_n^{(k)})}{p(x_{n+1}|x_n^{(k)})} \right] \tag{5}$$

This measure incorporates causal relationships by relating delayed (embedded) states, $x_n^{(k)}$ and $y_n^{(k)}$, to the state x_{n+1}, and quantifies the incorrectness of assuming independence between the two processes x and y. In short, the transfer entropy tells us the deviation from the expected entropy of two completely independent processes.

The transition probabilities can be systematically measured from the time series by coarse graining the phase space.

$$T_{Y\to X} = \mathrm{Max}\{T_{Y\to X}^{(k)}\}$$

They use the length of history (k) that maximizes transfer entropy.



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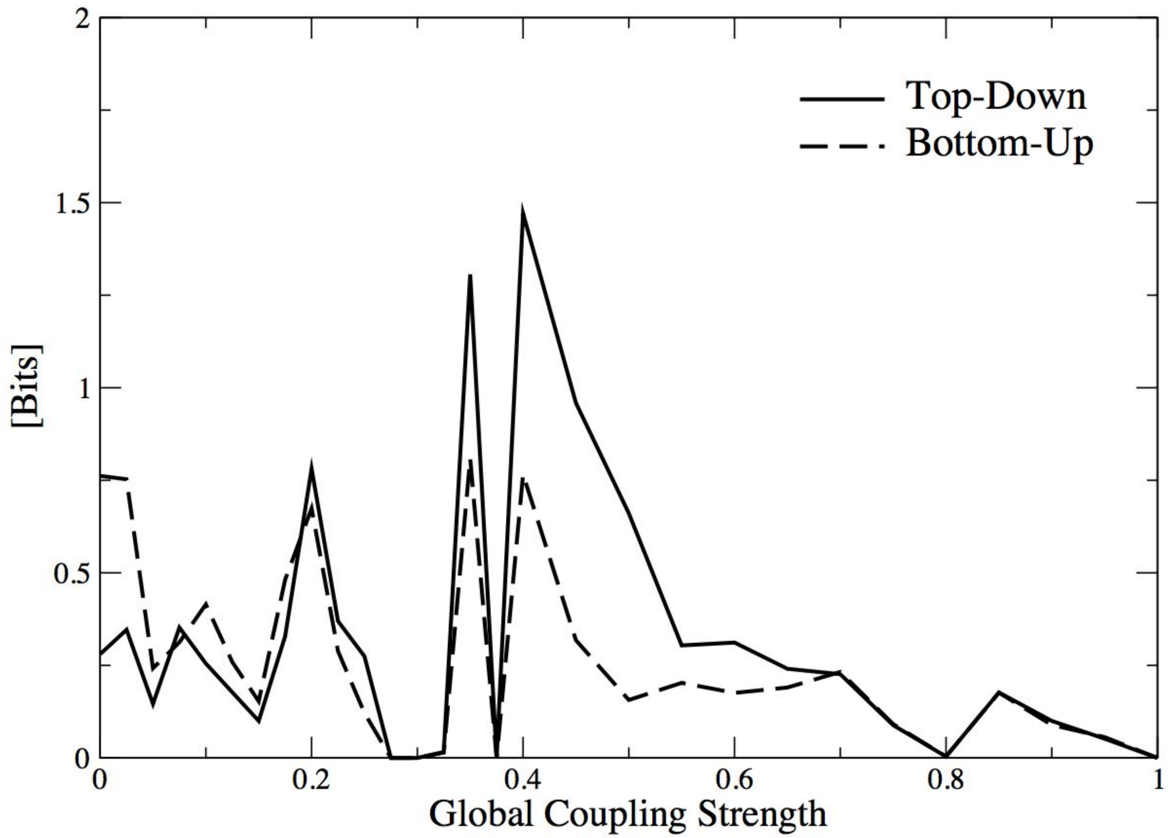
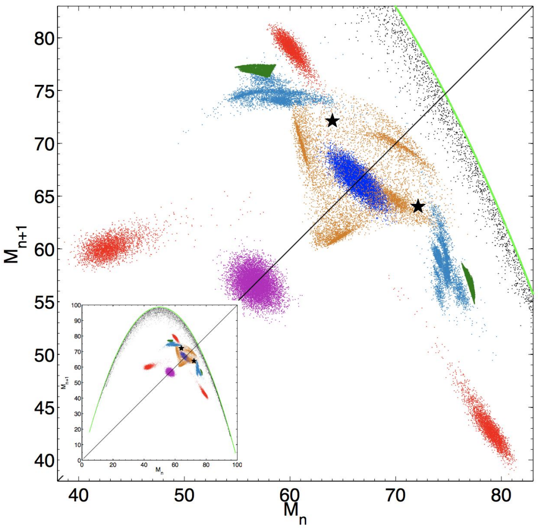


Figure 4: Top-down, $T_{M\rightarrow X}$ (solid), and bottom-up $T_{X\rightarrow M}$ (dashed), causal information transfer for varying global coupling strength ϵ of a system of coupled logistic maps.



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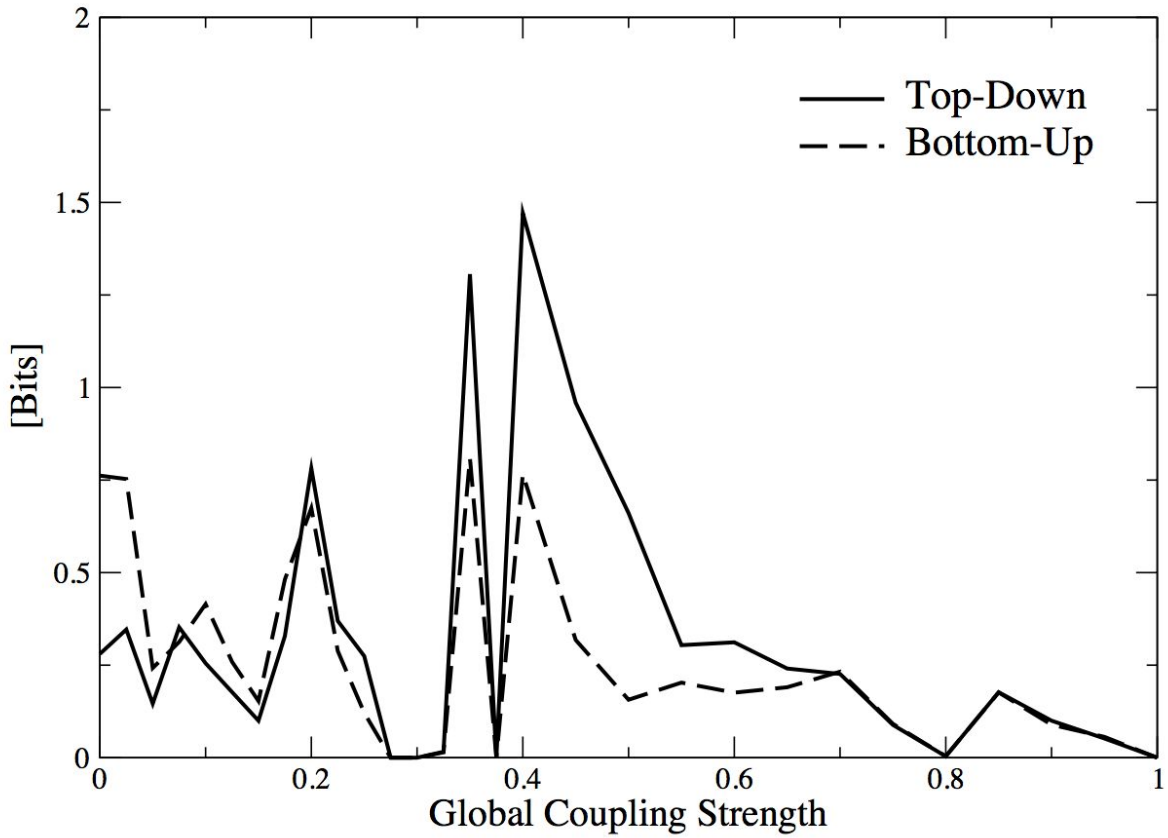

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Is this correct?
"In general, the trends observed indicate that each time a collective state emerges, causal information transfer is dominated by information flow from global to local scales."

Why is this toy model important?

- The authors hypothesize a transition in causal structure, from bottom-up to top-down, was the critical step in the origin of life
  - replicating molecules → populations of molecules in compartments
  - unlinked replicators → chromosomes
  - RNA → RNA + DNA + protein

- The origin of life is associated with the emergence of a collective contextual information processing system with top-down causal efficacy over the matter it is instantiated in
- Multicellularity emerges from the same process
- To understand these transitions we need better ways to understand the degree to which the whole dictates the parts and the parts dictate the whole