Is biological evolution open-ended?

- some speculations to be discussed -

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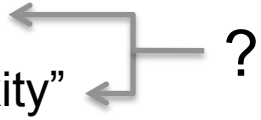
Open-Ended Evolution

A vast literature with hundreds of references…

- Two main definitions:
  - OEE ~ “Continuous generation of novelty”
  - OEE ~ “Continuous generation of complexity”



- A general claim
  - (Real) life is open-ended …
- BUT: 100% of the references come from the alife community. OEE is *NOT* in the scope of biology nor of evolutionary biology…

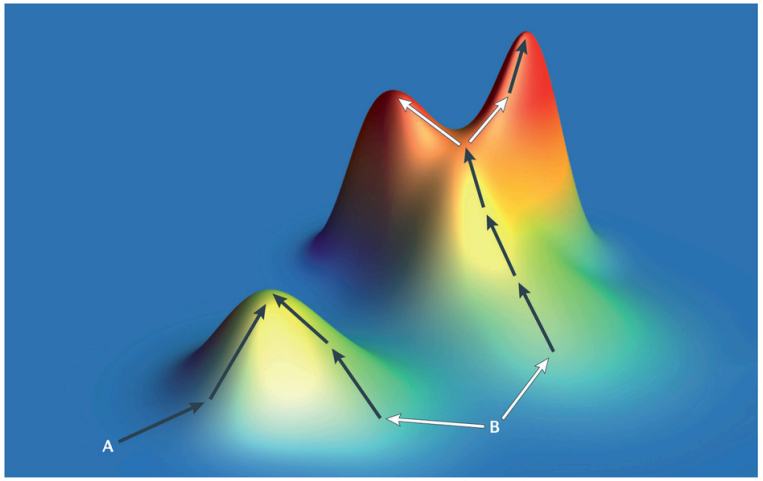
→ *What can we learn from this “paradox”?*

→ *Does it help to choose a definition?*

→ *Is life really open-ended?*

First answer: Evolutionary biologists mainly focus on stable states

- Evolutionary stable strategy theory: An approach to mathematically modelling evolution that defines equilibrium positions as positions at which, if all individuals are using the same strategy, invasion by rare individuals who adopt a different strategy is impossible. (Hurst, 2009)
- Similarly, most mathematical/empirical models focus on the evolutionary dynamic when reaching a stable predefined optimum (e.g., Wright-Fisher model, Wright's fitness landscapes)
- Selection is often considered as a stabilizing force (purifying selection), This effect can be quantified by measuring the dN/dS ratio between pairs of extant organisms



[Palmer & Kishony, 2013]

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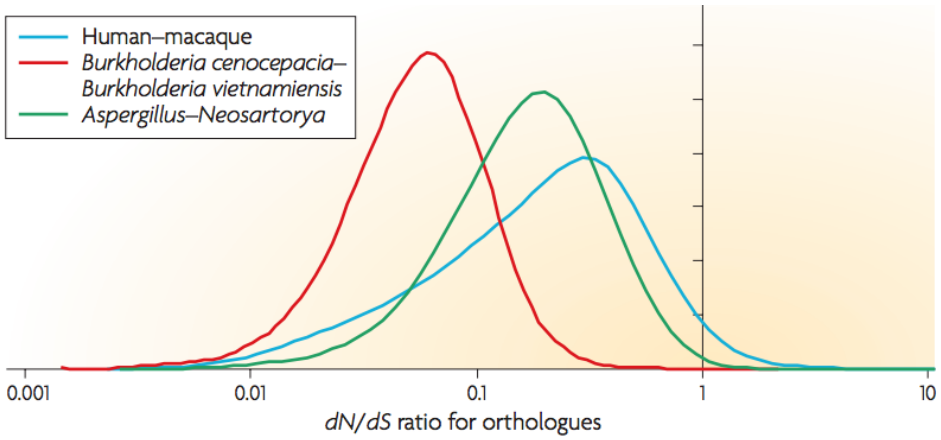

[Koonin & Wolf, 2010]

But novelty is pervasive in evolutionary biology…

- [Kimura, 1991]: “Neutral theory claims that the overwhelming majority of evolutionary changes at the molecular level are not caused by selection acting on advantageous mutants, but by random fixation of selectively neutral of very nearly neutral mutants through the cumulative effect of sampling drift (due to finite pop number) under continued input of new mutations.”
- [Bull *et al.,* 2005]: “Quasispecies are clouds of genotypes that appear in a population at mutation–selection balance. This concept has recently attracted the attention of virologists, because many RNA viruses appear to generate high levels of genetic variation that may enhance the evolution of drug resistance and immune escape.”
- [Loewe, 2008]: “negative (and positive) selection in such a [co-evolutionary] system will never rests.”

→ But no trace of something like an OEE concept… Why?

Second answer: Not all forms of novelty are equivalent

- Actually that's also the case in alife…
  - [Bianco & Nolfi, 2004]: OEE ~ "major novelty"
  - [Rasmussen *et al.*, 2004]: OEE ~ "adaptive novelty"
  - [Taylor, 1999]: OEE ~ "an indefinite variety of phenotypes are attainable through the evolutionary process, rather than continuous change being achieved by, for example, cycling through a finite set of possible forms"

  → *Is there something like classes of novelty?*
- Among all kinds of biological novelty, two are closer to the OEE concept:
  - Co-evolution, red-queen effect… but is it really unbounded? → back to ESS…
  - [Szathmary & Maynard-Smith, 1995]'s major evolutionary transitions which "involve[d] changes in the way information is stored and transmitted"
- Could OEE be the emergence of novelty leading to new individuality?
  - The definition of what is an individual continuously changes during evolution

Table 1. Revised major transitions

Origin of:	Formation, maintenance, transformation phases	Transition in individuality	New type of information storage, use, and transmission	Limited transitions
Protocells	1. Autocatalytic networks on the rocks cooperate 2. Naked genes escape into compartments 3. Chromosomes form	MLS1 on the rocks MLS2 in compartments Chromosomes as conflict mediators	Catalysts based on informational replication arise Genetic information encapsulated in cells	
Genetic code and translation: prokaryotic cells	1. Limited coding before translation (coenzyme amino acids and peptides) 2. Early ribosomes and primitive translation 3. Vocabulary extension by bacterial sex	Establishment of symbiotic autocatalytic molecular networks, including complementary subcodes	Symbolic as opposed to earlier iconic hereditary system (code) Coded sexuality	21st and 22nd amino acids (selenocystein and pyrrolisine) Highly polyploid bacteria
Eukaryotic cells	1. Fusion–fission cycle (early sex) 2. Mitochondrial symbiont (before or after phagocytosis) 3. Nucleus, meiosis, and mitosis	Different cells come and stay together as a higher level whole	Genome composed of functionally synergistic compartments Separation of transcription from translation	Within-cell soma and germ (ciliates)
Plastids	1. Engulfment of plastids 2. Transfer of plastid genes to nucleus 3. Posttranslational import and regulation of division	Different cells come and stay together as a higher level whole	Genome composed of functionally synergistic compartments	Tertiary plastids *Paulinella*
Multicellularity (plants, animals, fungi)	1. Size advantage from cohesion 2. Programmed regulation of cell division 3. Soma and early-sequestered germ line	Cohesive multicellularity allows for differentiation and division of labor	Epigenetic inheritance systems with high hereditary potential	Multicellularity in other lineages Multi-multi symbioses (e.g., lichens)
Eusocial animal societies	1. Origin of societies 2. Control of conflict (dominance, punishment, policing) 3. Dimorphic reproductive and nonreproductive castes	Formation of (super)organisms	Animal signaling and social learning	Unicolonial ant supercolonies
Societies with natural language	1. Confrontational scavenging, first words 2. Eusociality (grandmothers) and protolanguage 3. Cultural group selection and syntax	Non-kin, large-sized cooperation based on negotiated division of labor Food sharing and reproductive leveling Cultural groups	Symbolic communication with complex syntax	Animal cultures

Limited transitions are cases in which the formation and the maintenance of the units did not lead to vast adaptive radiations as seen in phylogeny. For example, ciliates with micro- and macronuclei are important, but they do not match the impact of segregated soma and germ in the eukaryotic multicells, and the same holds for other examples in this table. It is fair to say that these evolutionary novelties have been potentially major transitions that remained in bud so far. Some of these buds may flower, however, in the (hopefully) billions of years to come.

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What next?

[Szathmary, 2014]

Conclusion: if OEE~ emergence of individuality, can life be open-ended?

What neutral theory tells us:

- Mutations giving an advantage S have a fixation probability proportional to N_e (fixation probability ~N_eS) with N_e : effective population size…

What Major Transition theory tells us:

- "Entities that were capable of independent replication before the transition can only replicate as part of a larger unit after it" [Szathmary & Maynard-Smith, 1995].
- As the number of transitions increases, the total number of elements necessary to implement N individuals increases exponentially → N_e decreases exponentially

→ With a "universe" of M elements, one can only "implement" a maximum of $M/2^l$ individuals at level l… Thus the evolution of new transitions will rapidly exhaust the possibility of ***any*** system (including the biosphere) because selection will quickly become inefficient…

→ Some "tricks" may exist (e.g., exponential increase of S, rank-based selection, other?). Whether they enable OEE is an open question…