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## The Complexity Ratchet

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The evolutionary origin of biological complexity is a recurrent matter of debate. In short, two general categories of explanations are proposed in the literature. Neutralist ones state that the increase of complexity is due to random variations given that the initial complexity was close to zero. On the opposite, selectionist ones state that it is due to selection, complex organisms being fitter than simple ones. One of the central difficulties is that this debate is mainly based on thought experiments, experimental assays lacking to test these different hypotheses.

With this idea in mind, we used the Aevol in silico experimental evolution platform ([www.aevol.fr](http://www.aevol.fr)) to design an in silico experiment able to test the selective/neutralist hypotheses [1]: We evolved populations of organisms in two different environments, one designed to enable survival of the simplest possible organisms (i.e. organisms which genomes contain only one gene), the other designed to favor complex organisms (i.e. organisms which genomes contain a virtually infinite number of genes). By repeatedly evolving organisms in these two conditions, we were able to quantify the evolution of complexity – complexity being here measured as the amount of information in the genomes and in the proteomes.

Surprisingly, in the simple environment we observed that complex organisms evolve in more than three fourths of independent replicates. Moreover, when we compared the fitnesses of the simple individuals to the fitnesses of the complex individuals, we observed that simple organisms ended up with very high fitnesses while the fitnesses of complex organisms were typically 10 to 100 times lower, showing that complexity increase is not due to direct selection. Measurements of robustness and evolvability also showed that complex organisms are neither more robust nor more evolvable than simple ones, also excluding indirect selection from triggering the increase of complexity. Finally, a comparison of organisms that evolved in simple and complex environments showed that their complexities were of the same order of magnitude. This shows that complexity can accumulate even in conditions where it is not selected or even counter-selected! However, we also observed that in the absence of selection, complexity quickly drops in all situations showing that selection is an active force in the process of complexity accumulation. All these observations show that complexity increase is due to a “complexity ratchet”: each event of gene acquisition creates the potential for the acquisition of more genes, ultimately pushing evolution towards complex solutions even when the environment is simple. More precisely, the complexity ratchet is due to sign epistasis: in a simple environment a simple organism can improve its fitness through different mutational paths, some (e.g., sequence divergence) leading to simple organisms and some (e.g., gene duplication-divergence) leading to complex ones. Both paths are initially favorable but in the genetic background of complex organisms, the first one becomes highly deleterious. Hence, complex organisms cannot switch back to simplicity, even if this would be ultimately highly favorable. On the opposite, they slowly improve by accumulating new genes, each gene acquisition making the ratchet click further and pushing complexity to an increase.

## References

- [1] V. Liard, D.P. Parsons, J. Rouzaud-Cornabas, G. Beslon (2020) The complexity ratchet: Stronger than selection, stronger than evolvability, weaker than robustness. *Artificial life*, 26(1), 38-57.